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BENEFIT OF MICROPHYTIC CRUST INOCULATION AND ARBUSCULAR MYCORRHIZAL FUNGI ON PRODUCTIVITY OF VAM-DEPENDENT FORBS

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PREVIOUS WORK - FY95

In the previous year of funding, FY 1995, further investigation of interaction between microphytic soil crust organisms and arbuscular mycorrhizal fungi was initiated (MIPR W2V5AA51113582). This work effort had two primary objectives: 1) to evaluate changes in plant root morphology in response to inoculation with microphytic crusts and arbuscular mycorrhizae, and 2) to determine the relative benefit of mass-propagated algal inoculum and arbuscular mycorrhizal inoculum on the growth and nutrient content of five mycorrhizal-dependent arid-land shrub species. By October 1995, the work was well underway but not yet complete (see Pendleton and Pendleton 1995). This report will discuss subsequent progress made in meeting those objectives.

Objective I. Evaluate changes in plant root morphology in response to inoculation with microphytic crusts and arbuscular mycorrhizal fungi.

Work completed in 1993 found significant differences among soil and mycorrhizal treatments in root/shoot ratios, indicating that plants altered their allocation to root function in response to these variables (McArthur, Pendleton and Pendleton 1993). Quantification of root architecture was initiated to determine whether plant species used in the 1993 experiment altered root architecture in response to inoculation with microphytic crusts and mycorrhizal fungi, or merely reduced overall resource allocation to root function. Methodology and results for three of the five plant species were previously reported (Pendleton and Pendleton 1995). Since that time, the final two plant species have been examined and the data tabulated. Results for the complete experiment, inclusive of *Gaillardia pulchella* and *Bromus tectorum*, are given below.

Methods--Roots from the 1993 experiment were washed clean of debris and stored in 70% denatured ethanol pending analysis of root architecture. Quantification of root architecture proceeded as follows. Roots were cut into 1-2 cm segments and dispersed over a three cm grid in a shallow plexiglass tray. Total root length was calculated using a modified line intersect method developed by Tennant (1975). Root diameters of 50 random pieces were measured to the nearest 0.1 mm using an ocular micrometer. Specific root length was calculated as meters root length per gram dry root weight. Data were recorded on disk and analyzed using SAS version 6.11 for the personal computer. The model used was a 3 x 2 factorial with soil treatment and mycorrhizal

inoculation as main effects. Mean separations were accomplished using the Student-Newman-Keuls multiple range test.

Results--Statistical analysis revealed that crust additions significantly affected all three root variables (table 1). Total root lengths of *Bromus tectorum* (BRTE), *Gaillardia pulchella* (GAPU), and *Sphaeralcea munroana* (SPMU) plants were significantly increased by crust additions (tables 2, 4, & 6). The same trend was observed for *Sitanion hystrix* (SIHY) plants, although not statistically significant (table 5). In contrast, total root length of *Coleogyne ramosissima* (CORA) was smallest in the mixed crust treatment (table 3). Total root length, taken alone, is not so much a measure of root architecture as it is a reflection of plant root biomass (compare with root biomass figures in Final report:MIPR 94N107). The two variables are highly correlated ($p=0.0001$), with R^2 values ranging from 0.63 in CORA to 0.93 in GAPU (Fig. 1).

Inoculation with arbuscular mycorrhizal fungi (AMF) significantly affected total root lengths in BRTE, GAPU, and SIHY plants. Nonmycorrhizal plants of these species had significantly longer total root lengths in all soil treatments (tables 2, 4, &5). Again, this correlates well with root biomass figures previously reported. AMF had no significant effect on either CORA or SPMU plants.

Total root length, when divided by biomass, becomes specific root length, a measure of allocation to fine roots as compared to larger transporting roots (a better measure of root architecture). A high specific root length corresponds to a proportionately finer or lighter root mass. In the crust experiment, specific root length significantly decreased with the addition of crust material in BRTE ($p=0.0017$), GAPU ($p=0.0001$), SIHY ($p=0.0057$), and SPMU ($p=0.0001$). The same trend was also observed in CORA ($p=0.1240$), indicating proportionately less investment in fine feeder roots by plants growing in the more nutrient-rich crusted soils (tables 1-6).

The addition of mycorrhizal inoculum also resulted in decreased specific root length of CORA plants in all soil treatments ($p = 0.0230$), of GAPU plants in all but the mixed crust soil ($p=0.0001$) and of SPMU plants in crusted soils (nonsignificant), indicating fewer fine roots were produced by mycorrhizal plants under these conditions (tables 3,4, & 6). In GAPU plants, the interaction between soil treatment and mycorrhizal inoculation was significant, resulting in an ever widening difference in specific root lengths of mycorrhizal and nonmycorrhizal plants as soil fertility decreased (table 4). Nonmycorrhizal plants produced proportionately finer roots as soil fertility declined whereas mycorrhizal roots remained fairly constant. SIHY plants were completely opposite in response, mycorrhizal plants having much higher specific root values in all soil treatments (table 5). This was particularly surprising since mycorrhizal SIHY

Table 1. Attained significance values from ANOVA's of three root variables. Soil type and mycorrhizal inoculation (AMF) were used as main effects in the model.

Species/effects	Total root length	Specific root length	Root diameter
BRTE			
Soil treatment	0.0080	0.0017	0.0003
AMF treatment	0.0007	0.4402	0.0004
Soil x AMF	0.2966	0.2993	0.0047
CORA			
Soil treatment	0.0004	0.1240	0.0002
AMF treatment	0.5806	0.0230	0.9633
Soil x AMF	0.8265	0.9849	0.0989
GAPU			
Soil treatment	0.0001	0.0001	0.0058
AMF treatment	0.0081	0.0001	0.0317
Soil x AMF	0.2710	0.0002	0.0061
SIHY			
Soil treatment	0.2598	0.0057	0.4615
AMF treatment	0.0008	0.0001	0.0012
Soil x AMF	0.9137	0.0363	0.0083
SPMU			
Soil treatment	0.0001	0.0001	0.0491
AMF treatment	0.4475	0.1338	0.8285
Soil x AMF	0.1961	0.1484	0.3988

Table 2. Root variable measures for *Bromus tectorum* plants grown in three soil treatments. Half of the plants were inoculated with mycorrhizal fungi. Letters denote significant differences between mean values for soil and mycorrhizal (AMF) treatments. The interaction term for root diameter was significant. See text for an explanation.

A. Total root length

Soil treatment	+ AMF	- AMF	Soil treatment mean
Mixed crust	13662.0	36043.5	24852.8 a
Crust over sand	9181.6	21816.6	15499.1 ab
Blow sand	5571.0	12978.2	9274.6 b
AMF treatment mean	9471.5 a	23612.8 b	

B. Specific root length

Soil treatment	+ AMF	- AMF	Soil treatment mean
Mixed crust	14496.4	19475.8	16986.1 a
Crust over sand	24237.5	25373.0	24805.3 b
Blow sand	24422.2	22500.4	23461.3 b
AMF treatment mean	21052.1 a	22449.7 a	

C. Root diameter*

Soil treatment	+ AMF	- AMF	Soil treatment mean
Mixed crust	0.1660	0.1370	0.1515 a
Crust over sand	0.1410	0.1186	0.1298 b
Blow sand	0.1420	0.1460	0.1440 a
AMF treatment mean	0.1500 a	0.1339 b	

* Significant interaction term

Table 3. Root variable measures for *Coleogyne ramosissima* plants grown in three soil treatments. Half of the plants were inoculated with mycorrhizal fungi. Letters denote significant differences between mean values for soil and mycorrhizal (AMF) treatments. Interaction terms were not significant.

A. Total root length

Soil treatment	+ AMF	- AMF	Soil treatment mean
Mixed crust	175.1	169.2	172.2 a
Crust over sand	300.5	340.4	320.5 b
Blow sand	281.7	298.2	289.9 b
AMF treatment mean	252.4 a	269.2 a	

B. Specific root length

Soil treatment	+ AMF	- AMF	Soil treatment mean
Mixed crust	4021.7	4847.4	4434.6 a
Crust over sand	4865.9	5857.3	5361.6 a
Blow sand	4745.5	5651.7	5198.6 a
AMF treatment mean	4544.3 a	5452.1 b	

C. Root diameter

Soil treatment	+ AMF	- AMF	Soil treatment mean
Mixed crust	0.336	0.362	0.349 a
Crust over sand	0.259	0.279	0.269 b
Blow sand	0.324	0.280	0.302 b
AMF treatment mean	0.306 a	0.307 a	

Table 4. Root variable measures for *Gaillardia pulchella* plants grown in three soil treatments. Half of the plants were inoculated with mycorrhizal fungi. Letters denote significant differences between mean values for soil and mycorrhizal (AMF) treatments. Significant interaction between treatment main effects were found for both root diameter and specific root length. See text for discussion of interaction.

A. Total root length

Soil treatment	+ AMF	- AMF	Soil treatment mean
Mixed crust	10796.5	14830.9	12813.7 a
Crust over sand	3989.4	4623.9	4463.5 b
Blow sand	3300.6	5626.4	4306.7 b
AMF treatment mean	6028.8 a	8360.4 b	

B. Specific root length*

Soil treatment	+ AMF	- AMF	Soil treatment mean
Mixed crust	9621.5	9166.8	9394.2 a
Crust over sand	10926.5	13516.8	12221.7 b
Blow sand	10846.5	16861.6	13854.0 c
AMF treatment mean	10464.8 a	13181.7 b	

C. Root diameter*

Soil treatment	+ AMF	- AMF	Soil treatment mean
Mixed crust	0.204	0.219	0.212 a
Crust over sand	0.222	0.179	0.201 a
Blow sand	0.239	0.220	0.230 b
AMF treatment mean	0.222 a	0.206 b	

* Significant interaction term

Table 5. Root variable measures for *Sitanion hystrix* plants grown in three soil treatments. Half of the plants were inoculated with mycorrhizal fungi. Letters denote significant differences between mean values for soil and mycorrhizal (AMF) treatments. However, significant interaction among treatment main effects was found for both root diameter and specific root length variables. See text for discussion of interaction.

A. Total root length

Soil treatment	+ AMF	- AMF	Soil treatment mean
Mixed crust	2245.9	5139.7	3692.8 a
Crust over sand	1921.0	4563.6	3242.3 a
Blow sand	1174.8	3326.6	2250.7 a
AMF treatment mean	1780.6 a	4343.3 b	

B. Specific root length*

Soil treatment	+ AMF	- AMF	Soil treatment mean
Mixed crust	9731.4	7718.4	8724.9 a
Crust over sand	16442.3	7853.2	12147.8 ab
Blow sand	20996.7	9154.8	15075.7 b
AMF treatment mean	15723.4 a	8242.2 b	

C. Root diameter*

Soil treatment	+ AMF	- AMF	Soil treatment mean
Mixed crust	0.2720	0.2630	0.2675 a
Crust over sand	0.2270	0.2730	0.2500 a
Blow sand	0.2140	0.2970	0.2555 a
AMF treatment mean	0.2377 a	0.2777 b	

* Significant interaction term

Table 6. Root variable measures for *Sphaeralcea munroana* plants grown in three soil treatments. Half of the plants were inoculated with mycorrhizal fungi. Letters denote significant differences between mean values for soil and mycorrhizal (AMF) treatments. Interaction terms were not significant.

A. Total root length

Soil treatment	+ AMF	- AMF	Soil treatment mean
Mixed crust	6128.0	8694.9	7411.5 a
Crust over sand	2697.7	2112.9	2405.3 b
Blow sand	3257.3	3038.1	3147.7 b
AMF treatment mean	4027.7 a	4615.3 a	

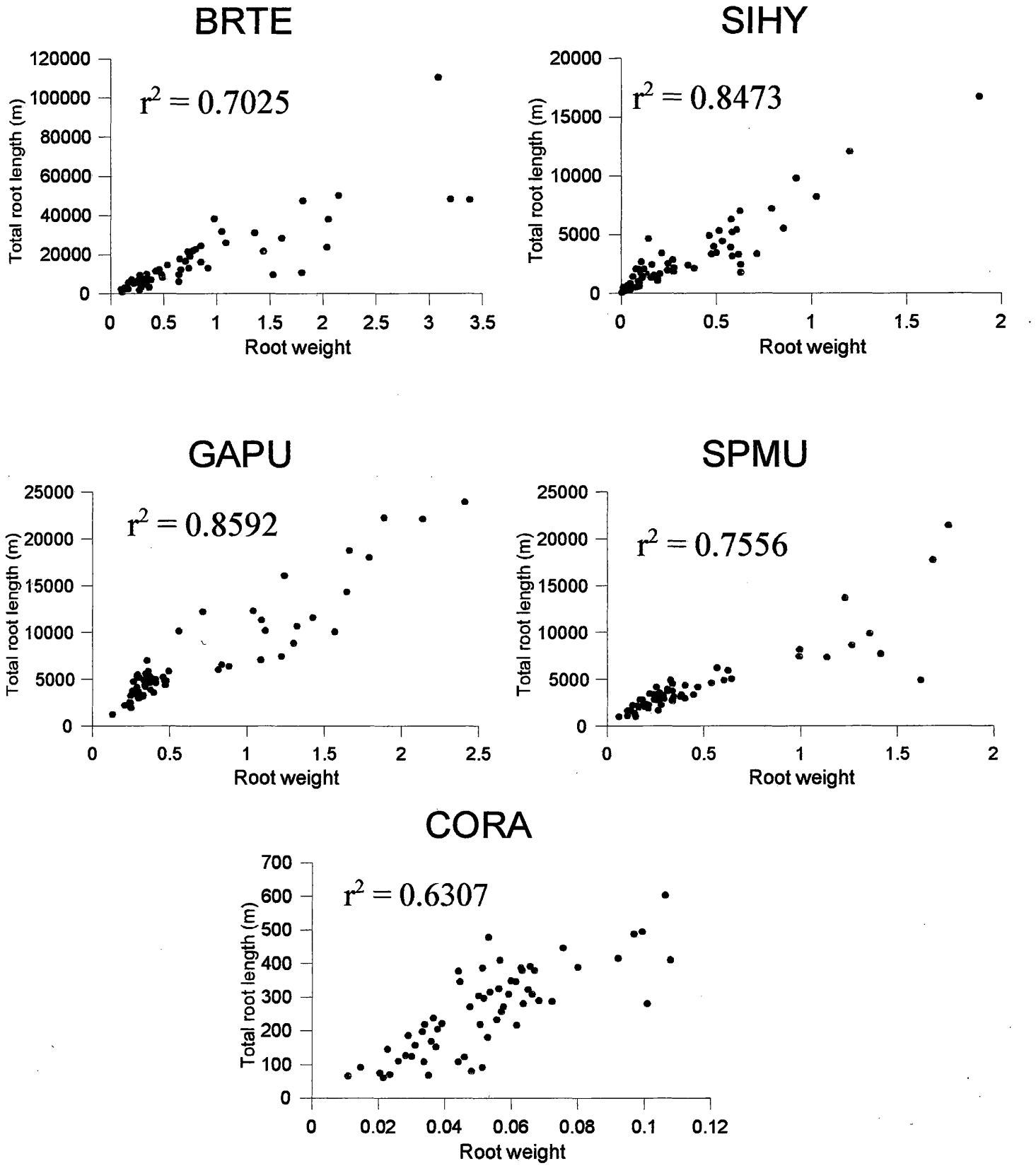
B. Specific root length

Soil treatment	+ AMF	- AMF	Soil treatment mean
Mixed crust	7848.3	9968.1	8908.2 a
Crust over sand	9433.7	11218.7	10326.2 a
Blow sand	13053.9	12201.6	12627.7 b
AMF treatment mean	10111.9 a	11129.4 a	

C. Root diameter

Soil treatment	+ AMF	- AMF	Soil treatment mean
Mixed crust	0.2250	0.2090	0.2170 a
Crust over sand	0.2520	0.2430	0.2475 b
Blow sand	0.2120	0.2300	0.2210 ab
AMF treatment mean	0.2297 a	0.2273 a	

Figure 1. Correlation of root weight with total root length



plants had a much smaller root mass than did nonmycorrhizal plants. Therefore, the addition of mycorrhizal inoculum to SIHY plants resulted in smaller root and shoot values, proportionately less allocation to root function, and finer roots. The addition of mycorrhizal inoculum had no significant effect on specific root length of BRTE plants.

Root diameter values varied widely and were more difficult to interpret than specific root length. Root diameters generally were greater for plants growing in mixed crust (CORA) or under a microphytic crust layer (SPMU). The addition of mycorrhizal inoculum had no significant effect on root diameter of either of these two species (tables 3 & 6). In SIHY, BRTE, and GAPU, significant interaction occurred between soil treatment and inoculation treatment with regards to mean root diameters (tables 1). For both BRTE and SIHY, mycorrhizal roots had the largest diameters in the mixed crust soil treatment, whereas nonmycorrhizal roots were largest in blow sand (tables 2 & 5). BRTE had an extremely fine mean root diameter in the crust over sand treatment, reflecting the numerous feeder roots mining the crust for nutrients. Mycorrhizal roots were larger in diameter than their nonmycorrhizal counterparts in the mixed crust (SIHY) or mixed crust and crust over sand (BRTE) soil treatments. This contrasts with GAPU plants (CORA also) where mycorrhizal roots were larger than nonmycorrhizal in the blow sand treatment (table 4). The GAPU root diameter data compliments the specific root length data in that both indicate that mycorrhizal roots showed less response to soil treatment than did nonmycorrhizal roots.

Conclusions--A brief summary of our research results on the responsiveness of root architecture is given below. Further analysis using plant size or mycorrhizal colonization as a covariate may yet reveal hidden patterns.

- Root architecture variables were significantly affected by both crust additions and inoculation with arbuscular mycorrhizal fungi.
- Plant species and life forms differed in their root architectural response to treatment variables.
- Total root length correlates strongly with root biomass.
- Proportionately less root biomass was invested in fine feeder roots in crusted soils as compared with the low nutrient blow sand.

- In non-grass species, mycorrhizal roots tended to be more coarse than nonmycorrhizal roots. In *Sitanion*, nonmycorrhizal roots tended to be more coarse, the difference being greatest in low nutrient soils.

- *Bromus tectorum* was unique in its proliferation of fine roots in the nonmycorrhizal crust over sand treatment block.

Objective II. Determine the relative benefit of mass-propagated algal inoculum and arbuscular mycorrhizal inoculum on productivity of mycorrhizal-dependent shrub species.

The purpose of this experiment was to determine the relative value of mass-produced algal inoculum and mycorrhizal inoculum for arid-land shrub growth and development. The effect of competition with cheatgrass (*Bromus tectorum*) was also evaluated. The ultimate goal of this and other ongoing research on microorganism interactions is to provide information that will aid revegetation efforts of disturbed arid lands.

Methods--Seed of five shrub species, *Ephedra viridis*, *Coleogyne ramosissima*, *Artemisia filifolia*, *Chrysothamnus nauseaosus* ssp. *hololeucus*, and *Artemisia tridentata* ssp. *tridentata*, representing both cold and mixed desert communities, was obtained from native populations in Utah. Cheatgrass seed (provided by S. Meyer) was collected from the Whiterocks area in Utah.

Algal inoculum, of the genus *Schizothrix* (also some *Todipothrix*), was obtained in concentrated slurry form from Dr. Jeffrey Johansen of John Carroll University. The slurry was suspended, pelletized, and dried according to the procedures described in MIPR 94N107:Final Report. Dried pellets were then ground to the consistency of meal, using a wheat grinder provided by Dr. Larry St. Clair of Brigham Young University. Ground pellets were stored at 4 C until needed.

For the mycorrhizal inoculum, soil was collected from beneath shrubs growing near Toquerville, Utah. Shrub species growing at this location included *Coleogyne ramosissima*, *Artemisia filifolia*, *Artemisia tridentata*, and one species of *Ephedra*. Spores were extracted by wet-sieving and decanting, followed by sucrose centrifugation (Daniels and Skipper 1982; Walker et al. 1982). Freshly-extracted spores were suspended in water and added to pots using a pipette. Replicate alliquots were decanted onto filter paper and spore counts made. Nonmycorrhizal treatments received an equal volume of killed (autoclaved) spore suspension combined with

microbial-containing washings that had passed a 25 micron sieve. An attempt will be made to identify fungal species used in the inoculum at a later date.

Soil used in the experiment was a bank sand purchased from Western Sand and Gravel in Spanish Fork, Utah. The soil had a pH of 8.5, conductivity of 0.4 mmhos/cm and plant-available nutrient concentrations of 4.7, 2.9, and 22.4 ppm for nitrate-N, phosphorus, and potassium, respectively. The sand was steamed for two hours at 77 C. Following steaming, sand was amended to one of three fertilizer levels (low, medium, and high) using Osmocote 17-7-12 formulated for 12-14 months continuous fertilization. The low fertility level had no additional fertilizer added. Medium and high treatment levels were amended to low (5 oz. per cubic foot) and high (9 oz. per cubic foot) values recommended by the manufacturer. Large Durapots (5 1/4 x 5 1/4 x 5 3/4 inches) by Hummert Int. were used in the experiment.

Plants were grown in one of four inoculation treatments; algal inoculation (a rate of approximately 100 g/m^2), mycorrhizal inoculation (50-100 spores), both algal and mycorrhizal inoculation, and a non-inoculated control. Mycorrhizal inoculum was added to the soil at a depth of 1-2 inches just prior to planting. Algal inoculum was sprinkled evenly over the top of the pot immediately following planting. Seeds of *Coleogyne* and *Ephedra* were pregerminated on moistened filter paper before planting. All other species were seeded, then thinned to one plant per pot upon emergence. Half of the pots were also planted with one seed of cheatgrass.

Plants were grown in a controlled-environment growth chamber at Brigham Young University. The temperature/light regime simulated that of a growing season, beginning with a March equivalent of 5 C nighttime temperature, a 15 C daylight temperature, and a 12 hr day length. This was increased until a summer regime of 15/25 C with a four hour midday temperature of 30 C and a 14 hr day length was reached. Temperature regimes were changed monthly, and water was supplied as needed. Only three replications per treatment combination would fit in the growth chamber at any one time, so the intent was to make at least one subsequent experimental run of approximately six months duration.

Plants were harvested following a growth period of approximately six months (25-27 weeks). Shoots were excised at ground level, dried at 65 C, and weighed. Roots were washed free of sand, dried, and weighed. Root/shoot ratios were subsequently calculated and the data entered on computer disk. Statistical analyses were accomplished using the GLM procedure of SAS version 6.11 for the personal computer (SAS Institute Inc. 1989). Survival data (the number of shrubs surviving in each treatment block) were analyzed using soil fertility and competition with cheatgrass as

the main effects. Growth effects were analyzed separately for each shrub species using fertility, competition, mycorrhizal inoculation, and algal inoculation as main effects. The effect of soil fertility was also addressed in a one-way model with mean separations using the Student-Newman-Keuls multiple range test.

Results--Cheatgrass growth at both medium and high fertilizer levels was prodigious enough to shade plants in the same or adjacent containers. This resulted in very few shrubs surviving at medium and high fertilizer levels. Shrub growth at all levels was severely affected by the proximity of large cheatgrass plants. Sufficient data were recovered to allow the formulation of broad conclusions regarding cheatgrass competition that will aid in designing a successful second run of this experiment.

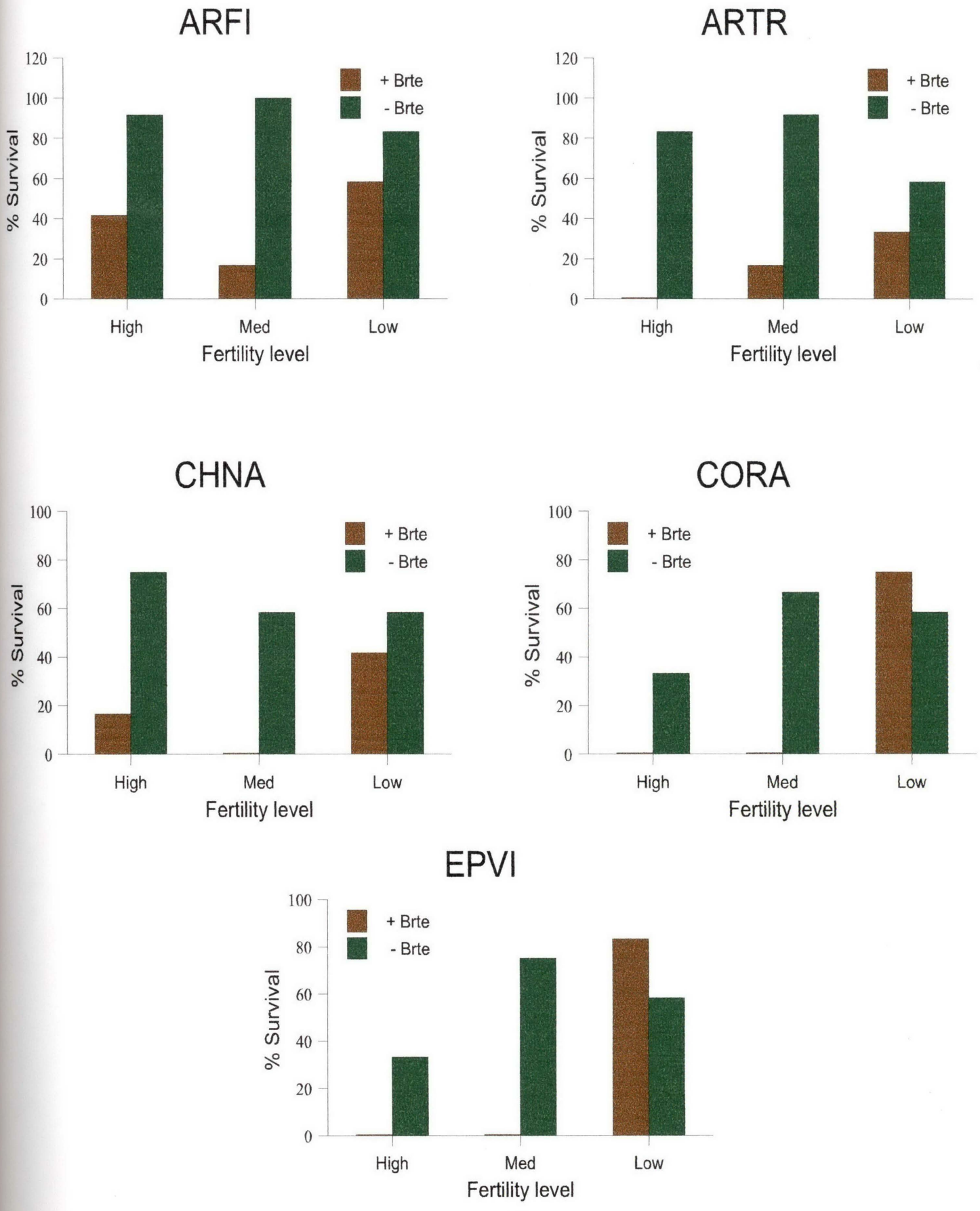
An analysis of shrub survival was undertaken using arcsin-transformed survival percentages for each shrub/treatment combination. Cheatgrass competition and soil fertility were used as the main effects. Both main effects and their interaction were significant (table 7).

Table 7. ANOVA table from analysis of shrub survival.

Source	df	SS	MS	F value	Pr > F
Fertility	2	0.55530	0.27765	4.17	0.0278
Competition	1	2.52675	2.52675	37.98	0.0001
Fert x comp	2	1.14454	0.57227	8.60	0.0015

Because of the significant interaction term, the effect of competition on shrub survival was subsequently assessed separately for each soil fertility level. Shrub survival was significantly reduced by the presence of cheatgrass at both high ($p=0.0071$) and medium ($p=0.0003$) fertility levels, but not at low ($p=0.6846$). Soil fertility did not significantly affect shrub survival in the absence of competition from cheatgrass (Figure 2).

Figure 2. Comparison of shrub survival with and without competition from BRTE.



Growth of surviving shrubs was greatly reduced in the presence of cheatgrass. Shoot and root growth of EPVI and CHNA, and root growth of CORA were significantly affected ($p < 0.05$), though all shrub species exhibited a similar trend.

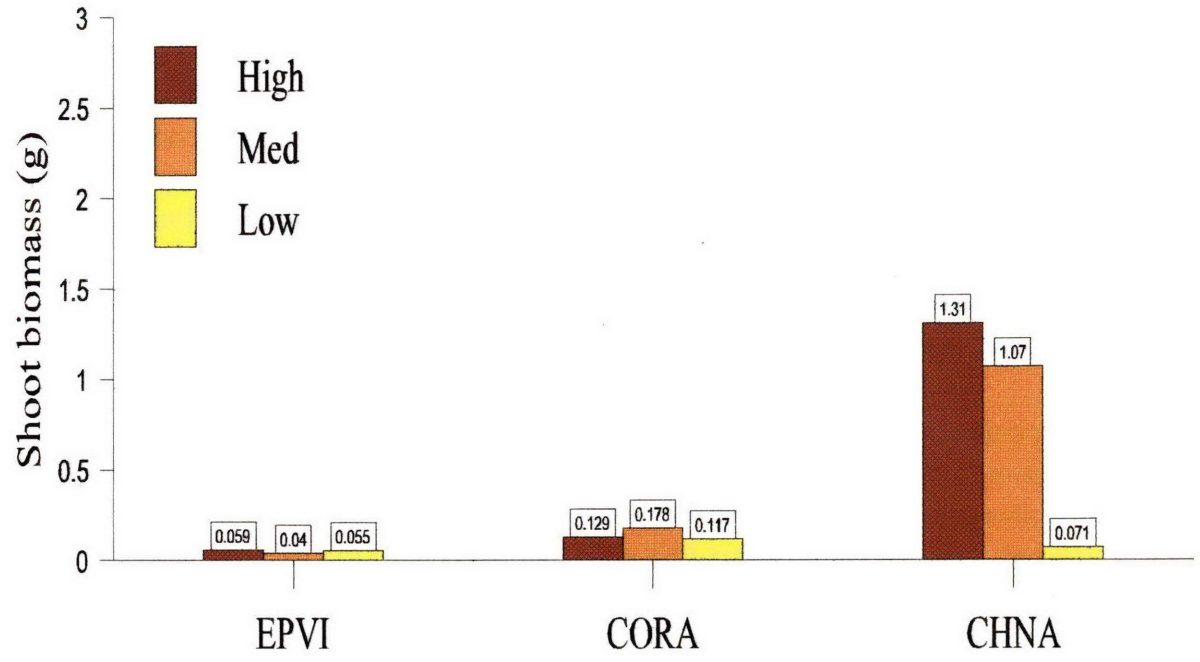
Visual assessment of shrub growth at the time of harvest indicated that plant growth at high and medium fertility levels was remarkably similar. Subsequent analyses confirmed this observation. Soil fertility significantly affected growth of ARFI, ARTR, CHNA, and BRTE (table 8), with medium and high-level plants growing larger than those at low fertility. The slower growing CORA and EPVI plants were only marginally affected. In only one case did plant growth at high and medium fertility levels differ. A couple of unusually large ARFI plants growing at the medium fertility level resulted in significantly larger ARFI growth at medium than at the highest fertility level (Fig. 3). For the purposes of this experiment, it appears that the high fertility level may be somewhat superfluous.

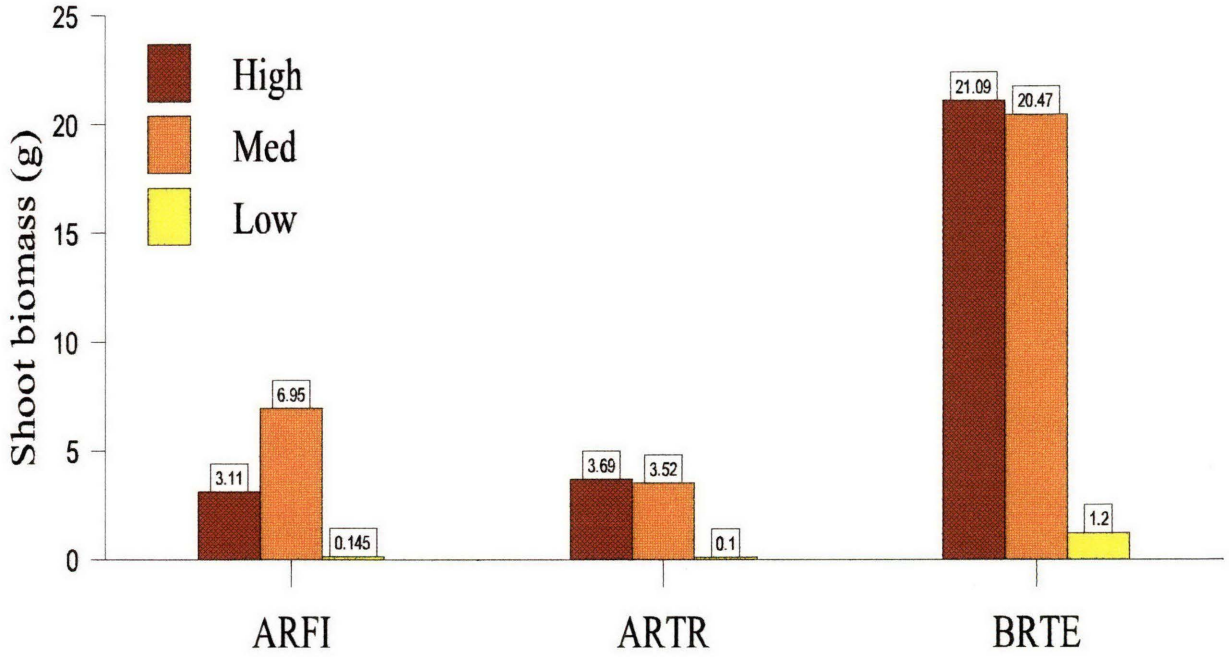
Table 8. Effects of soil fertility on plant growth. Attained significance values from the General Linear Models procedure.

	Shoot biomass	Root biomass	r/s ratio
BRTE	0.0001	0.0001	0.0021
ARFI	0.0001	0.0001	0.0004
ARTR	0.0003	0.0001	0.0001
CHNA	0.0072	0.0353	0.0325
CORA	0.4002	0.0424	0.5305
EPVI	0.4532	0.1817	0.0338

A complete presentation of experiment results can be found in Appendices I and II. Further interpretation of treatment effects is of questionable value, however. Shrub growth was profoundly affected by the random presence or absence of large BRTE plants in adjacent pots. This fact, coupled with the small number of experimental units in each treatment block, makes the results difficult to interpret and of dubious significance. Nevertheless, a few interesting trends are worth pointing out.

Figure 3. Plant growth at three soil fertility levels.





First, the presence of mycorrhizal inoculum appeared to enhance growth of EPVI at all fertility levels and of CORA and CHNA at the lowest fertility level. ARFI, ARTR, and BRTE showed no positive response to mycorrhizal fungi. Second, the addition of algal inoculum appeared to enhance growth in three shrub species. ARTR growth was enhanced at all fertility levels. The presence of algae appeared to benefit ARFI plants, particularly when competing with BRTE. And growth of CHNA at the low fertility level may have profited from the dual inoculation of algae and mycorrhizal fungi. The EPVI and CORA exhibited no positive response to algal inoculation. Finally, the shrubs seemed to group themselves somewhat in their response to experimental treatments. ARFI and ARTR were similar in their treatment responses, as were the slow-growing CORA and EPVI. CHNA tended to be intermediate in response.

Recommendations for the second run--Phase two of the shrub experiment is now in process. Four inoculation treatments are being used as in the previous run; algal inoculation, mycorrhizal inoculation, dual inoculation, and an uninoculated control. Only two fertility levels are being used, low and medium, as the high fertility level did not produce a significantly different growth response from that of the medium fertility level in the previous run. Competition with *Bromus* will be included at the low fertility level only. Ten replicate plants of each of the five species will be grown per treatment block. Plants will be grown in the greenhouse as opposed to a growth chamber. This will allow sufficient space between plants for uniform light interception and air circulation. The greenhouse has been cleaned, sprayed with a biocide, and equipped with new evaporative cooling pads. Inoculation procedures will be carried out as previously described and the plants harvested after 5-6 months growth.

CURRENT WORK - FY96

BENEFIT OF MICROPHYTIC CRUST INOCULATION AND ARBUSCULAR MYCORRHIZAL FUNGI ON PRODUCTIVITY OF VAM-DEPENDENT FORBS

Forbs comprise an important, though often understudied, component of western rangelands. Prized for their colorful contribution to western landscapes, forbs also play an important part in the diets of herbivorous wildlife, including the endangered desert tortoise. While precious revegetation efforts have focused primarily on the use of grass and shrub species, the use of herbaceous flowering plant seed in revegetation mixes has become increasingly common. As a result, the establishment requirements of forbs are becoming a research priority. The role of microphytic crust organisms and arbuscular mycorrhizal fungi in the establishment and reproduction of forbs remains largely unexplored. Data from our 1993 experiment demonstrate a consistent trend for mycorrhizal forbs to be larger in soils where crust material was present, but smaller in noncrusted sand. Studies by Belnap and Harper (1995), Harper and Pendleton (1993), and references therein also suggest that further research into the biological interactions of microphytic crust organisms, mycorrhizal fungi, and higher plant establishment will prove fruitful.

Previous experiments were designed to examine the effect of mass-propagated algal and VA fungal inocula on growth of shrub species. In this experiment, we examined the effects of these inocula, both singly and in combination, on the survival, growth, reproduction, and mineral content of five herbaceous plant species native to the Intermountain region. The objective of the study was to determine the relative benefits of these two inocula on plant productivity.

Methods-- Seed of five herbaceous plant species, *Penstemon palmeri* (PEPA), *Sphaeralcea coccinea* (SPCO), *Linum lewisii* (LILE), *Achillea millefolium* (ACMI), and *Hedysarum boreale*(HEBO), representing both cold and mixed desert communities, was used in the experiment. Seed was obtained from either Granite Seed Company in Lehi, Utah, or from Stan Kitchen of the Shrub Sciences Laboratory in Provo, Utah. All seed was collected from native sources.
Pelletized algal inoculum of the genera *Microcoleus* and *Nostoc*, originally grown by Susan Butters, was ground to the consistency of meal using a wheat grinder provided by Dr. Larry St. Clair of Brigham Young University. The inoculum was applied at a rate of 75 g/m^2 or approximately 1.6 g per pot, sprinkled evenly over the top of the pot at the time of planting.

Mycorrhizal inoculum was produced by pot culture. Soil collected from beneath shrubs growing near Toquerville, Utah, was planted with ornamental corn seed (lot #125) obtained from Carpenter Seed Co. When corn plants were mature, the stalks were excised and the soil-root mass removed from the pot and sliced into rough cubes of approximately 1 cm^3. Some of the inoculum thus produced was subsequently autoclaved for use in nonmycorrhizal treatments. Inoculum was applied 1-2 inches below the soil surface just prior to planting. One teaspoon (approximately 100 spores) of inoculum was used per pot.

Soil used in the experiment was a low fertility bank sand purchased from Western Sand and Gravel in Spanish Fork, Utah. The sand was steamed for two hours at 77 C. Following steaming, sand was amended to one of three fertilizer levels (low, medium, and high) using Osmocote 17-7-12 formulated for 12-14 months continuous fertilization and ammonium nitrate. All treatments received 2.4 g ammonium nitrate per 30 gallons of sand to raise the nitrogen level to 10 ppm. In addition, medium and high fertilizer levels were amended at a rate of 5 oz. and 9 oz. Osmocote per cubic foot, respectively, values recommended by the manufacturer. Olympian 300XL pots by Hummert Int. were used in the experiment.

Plants were grown in one of four inoculation treatments; algal inoculation, mycorrhizal inoculation, dual inoculation, and a non-inoculated control. All plant species were seeded, then thinned to one plant per pot upon emergence. Plants were grown in a thoroughly-cleaned, temperature-controlled greenhouse until mature and ready to harvest. Watering was accomplished by means of a capillary matting system. *Achillea* plants were grown for 10 weeks, *Penstemon* for 12 weeks, *Sphaeralcea* for 13 weeks, *Hedysarum* for 14 weeks, and *Linum* for 15 weeks.

Plants were harvested while still green and actively growing. Shoots were excised at ground level, dried at 65 C, and weighed. Roots were washed free of sand, dried, and weighed. Flowering stalks of *Hedysarum* were measured to the nearest cm, while those of *Sphaeralcea* were clipped, dried, and weighed. Minimal flowering in the other three species precluded data collection on reproductive biomass. The above-ground vegetative biomass of all five species is now being ground for analysis of mineral content.

The plant biomass data were entered on computer disk and analyzed using SAS version 6.11 for the personal computer (SAS Institute Inc. 1993). Species were analyzed separately using the General Linear Models procedure. Soil fertility, algal treatment, and AMF treatment were used as main effects in the model. Because of significant

interaction terms involving soil fertility, the effects of algal and AMF inoculation treatments were also analyzed separately by each soil fertility level. Survival data were analyzed using the ANOVA procedure with plant species as a blocking factor.

Results--A comprehensive presentation of experimental data and results of statistical testing, including attained significance values, treatment means, and survival data, are given in Appendices III, IV, V, and VI.

Survival--The effects of plant species and soil fertility on plant survival were highly significant (table 9). Overall survival of the different plant species ranged from 81.9% in *Achillea*, through 69.4 in *Sphaeralcea*, 50% in *Hedysarum*, and 49.3% in *Linum*, to 35.4% in *Penstemon*. Survival was greatest at low soil fertility and least at high soil fertility (Figure 4). The interaction between soil fertility and algal inoculation was significant (table 9). When survival data were analyzed separately for each fertility level, it was found that the use of algal inoculum significantly improved plant survival at medium ($p=0.0469$) and low ($p=0.0024$) soil fertility levels, though not at high ($p=0.3082$) (Figure 5).

Table 9. Results from ANOVA of plant survival data.

Source	df	Anova SS	Mean square	F value	Pr > F
Soil fertility	2	6.01410978	3.00705489	38.06	0.0001
Algal inoculation	1	0.31422546	0.31422546	3.98	0.0521
AMF inoculation	1	0.13370027	0.13370027	1.69	0.1998
Plant species	4	3.66638213	0.91659553	11.60	0.0001
Fert x algae	2	0.64268668	0.32134334	4.07	0.0236
Fert x AMF	2	0.28256408	0.14128204	1.79	0.1787
Algae x AMF	1	0.00689368	0.00689368	0.09	0.7690

Growth and reproduction--Soil fertility level had a significant effect on growth of all species used in the experiment (Appendix III). Both root and shoot systems grew larger with additions of Osmocote fertilizer. Plant growth at medium and high soil fertility

Figure 4. Plant survival as a function of soil fertility level.

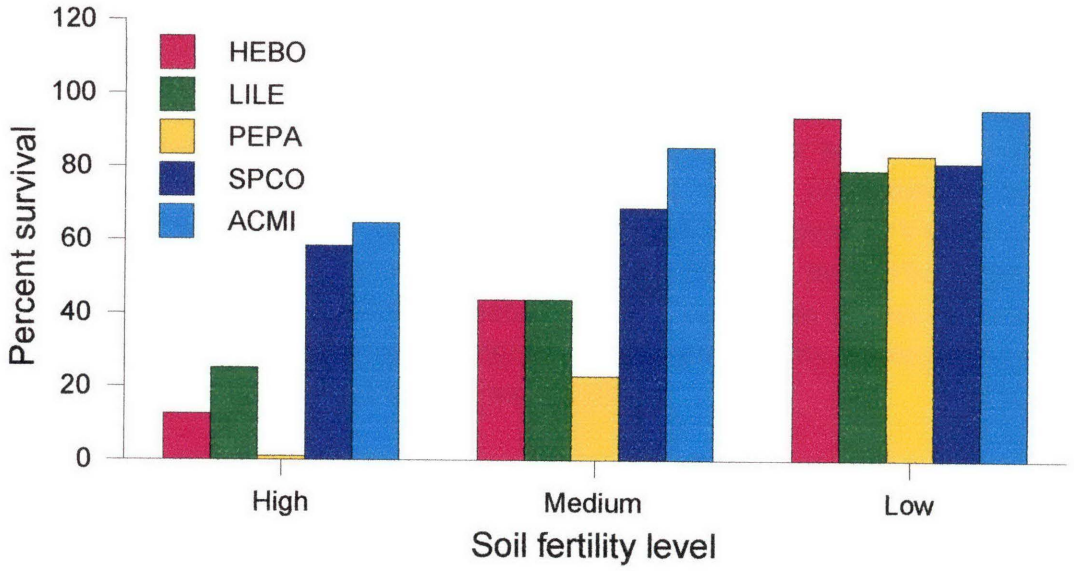
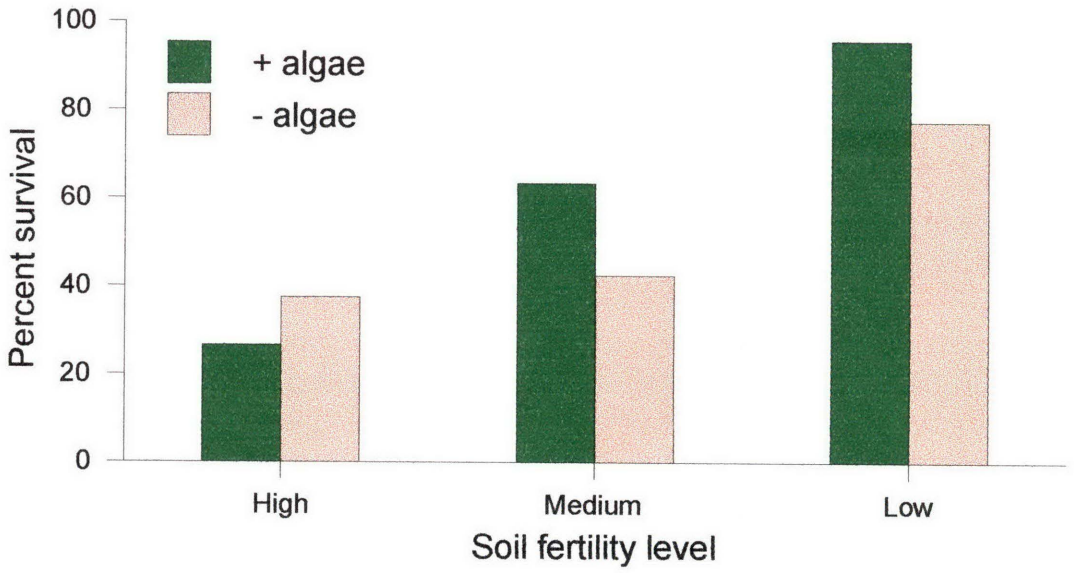


Figure 5. Effect of algal inoculation on plant survival.



levels did not differ significantly, with the exception of SPCO, where plants at the medium fertility level grew significantly larger. Nevertheless, all species tended to grow best at the medium fertility level (Figure 6).

Plant response to mycorrhizal inoculum fell into one of three categories; always positive, always negative, and variable, depending on soil fertility (Figure 7). Mycorrhizal *Linum* and *Sphaeralcea* plants were consistently larger than nonmycorrhizal plants in both shoot and root systems (Appendix V).The significance of this difference increased with decreasing soil fertility, mycorrhizae proving most beneficial at low soil fertility (Appendix IV). *Linum*, in particular, seemed to be hightly dependent on mycorrhizal fungi, growing significantly better in the presence of mycorrhizal inoculum, even at high soil fertility.

In contrast, *Hedysarum* plants responded negatively to additions of mycorrhizal inoculum (Figure 7). Indeed, only nonmycorrhizal plants survived at high soil fertility. Surprisingly, plants grew quite well, even at the lowest fertility level. Reponse to mycorrhizal fungi in this leguminous species may well have been different had rhizobial inoculum been included in the experiment.

Mycorrhizal response of *Achillea* and *Penstemon* plants varied with soil fertility level (Figure 7). In both species the presence of mycorrhizae appeared to inhibit growth at medium and high fertility levels, particularly in the absence of algae. This difference was not always significant, however (Appendix IV). At low fertility, both species responded positively to mycorrhizal inoculation, with the response being highly significant.

Growth response to algal inoculation was complex, having many significant interaction terms with both soil fertility (PEPA, SPCO, and ACMI) and mycorrhizal fungi (ACMI)(see Appendix III). Nonsignificant trends in HEBO and LILE also tended to differ with soil fertility. Biomass means for both these species tended to be larger in the presence of algae at medium fertility and lower in the presence of algae at low fertility (Figure 8a,b). Algal inoculum appeared to aid growth and survival of HEBO at high fertility. Only plants inoculated with algae survived in this soil treatment. In SPCO, inoculation with algae had a significant positive effect on plant growth at medium and high fertility levels, though not at low (Figure 8c). In contrast, PEPA plants tended to be smaller under algae at medium fertility (Figure 8d). In ACMI, the addition of algae improved plant growth of mycorrhizal plants at medium and high fertility levels and nonmycorrhizal plants at medium and low fertility levels.

Figure 6. Root and shoot biomass as a function of soil fertility level.

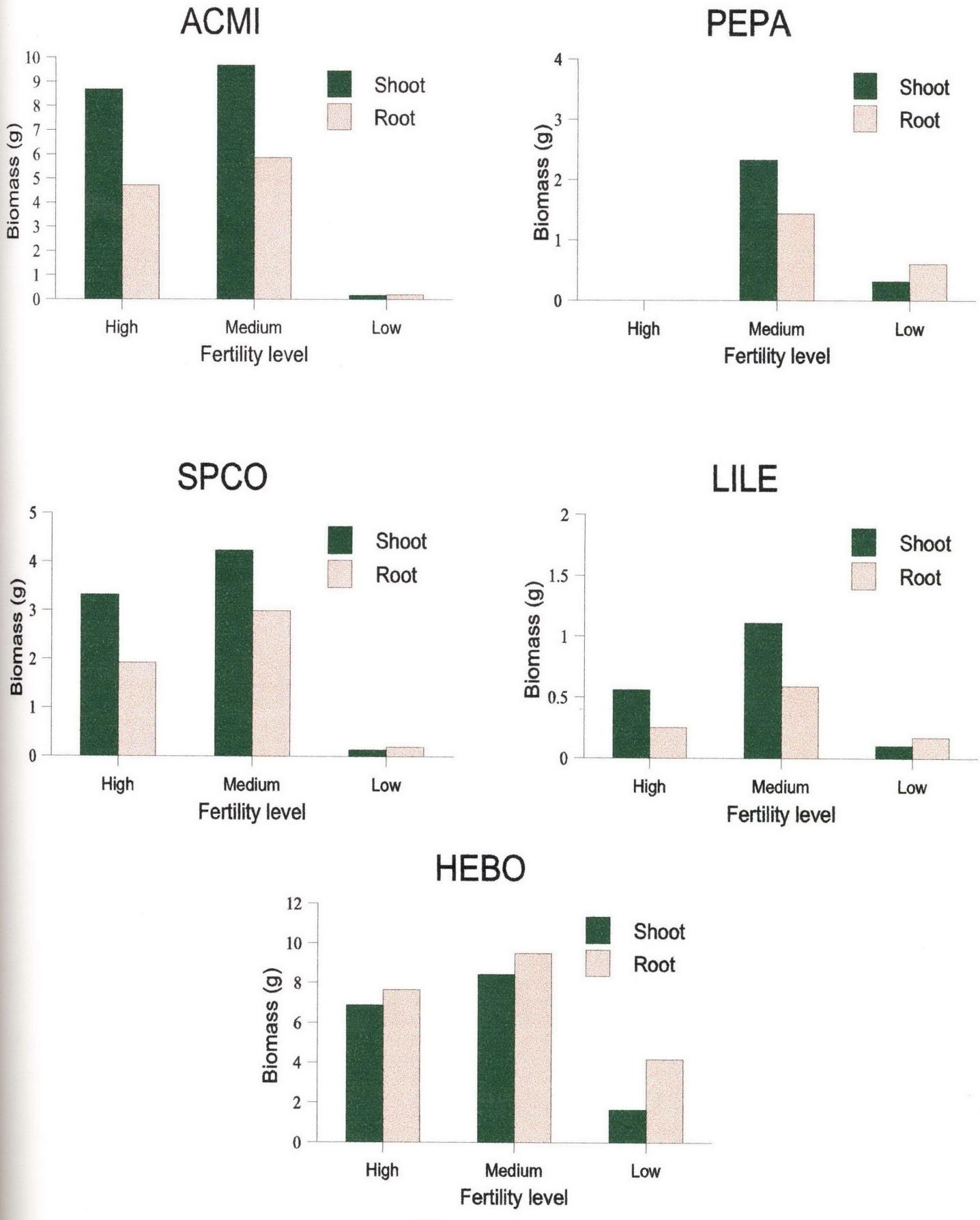


Figure 7. Shoot biomass of mycorrhizal and nonmycorrhizal plants.

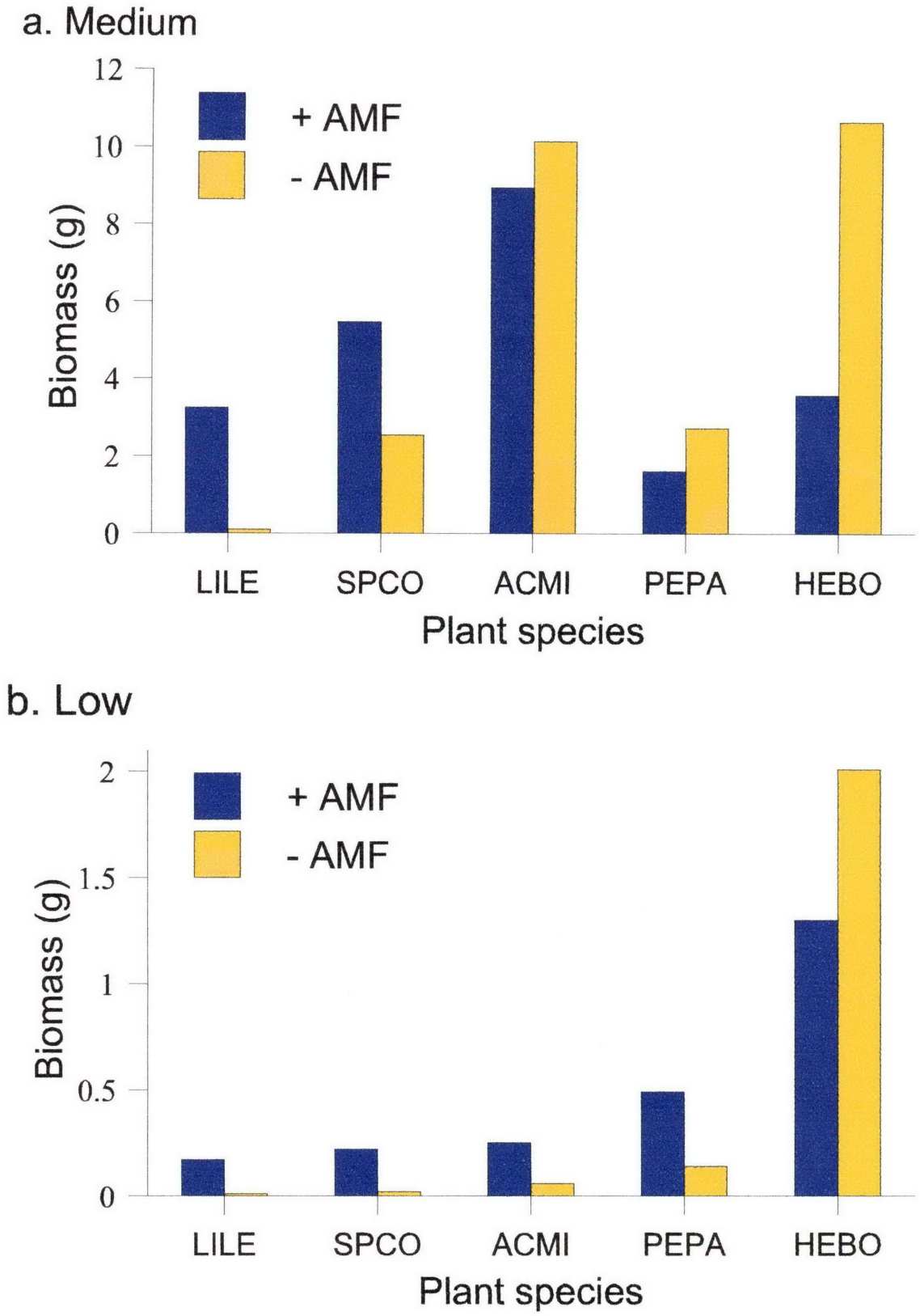
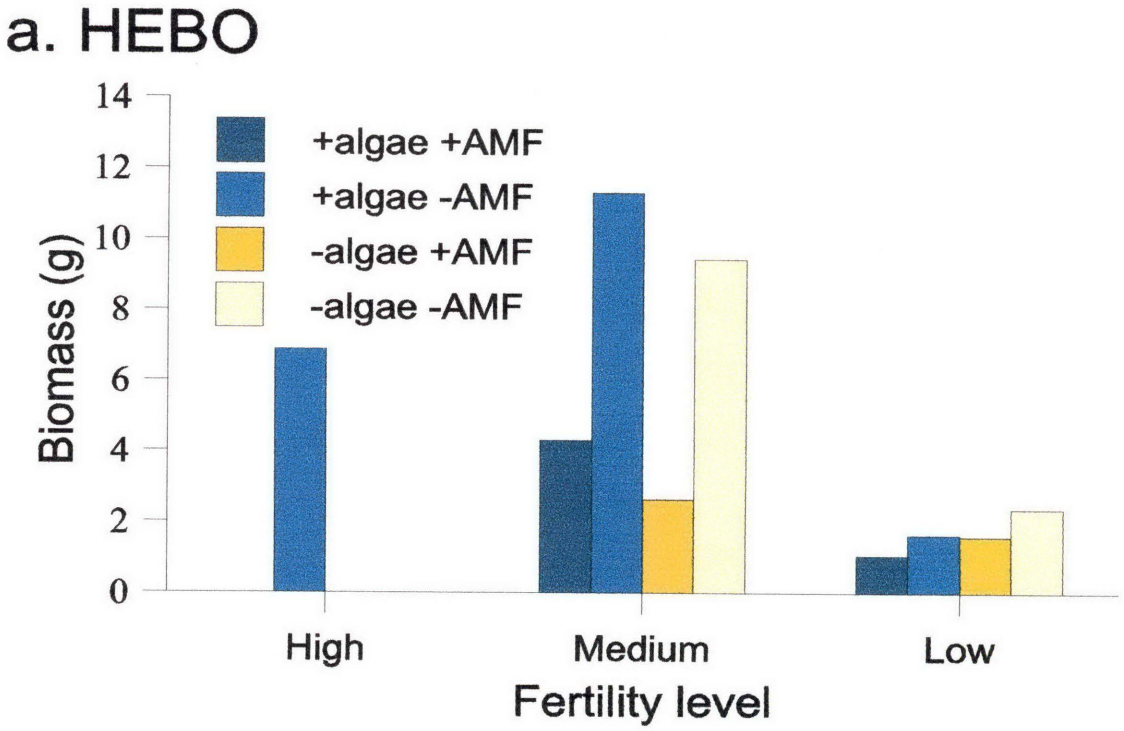


Figure 8. Effect of algal inoculation on shoot biomass.



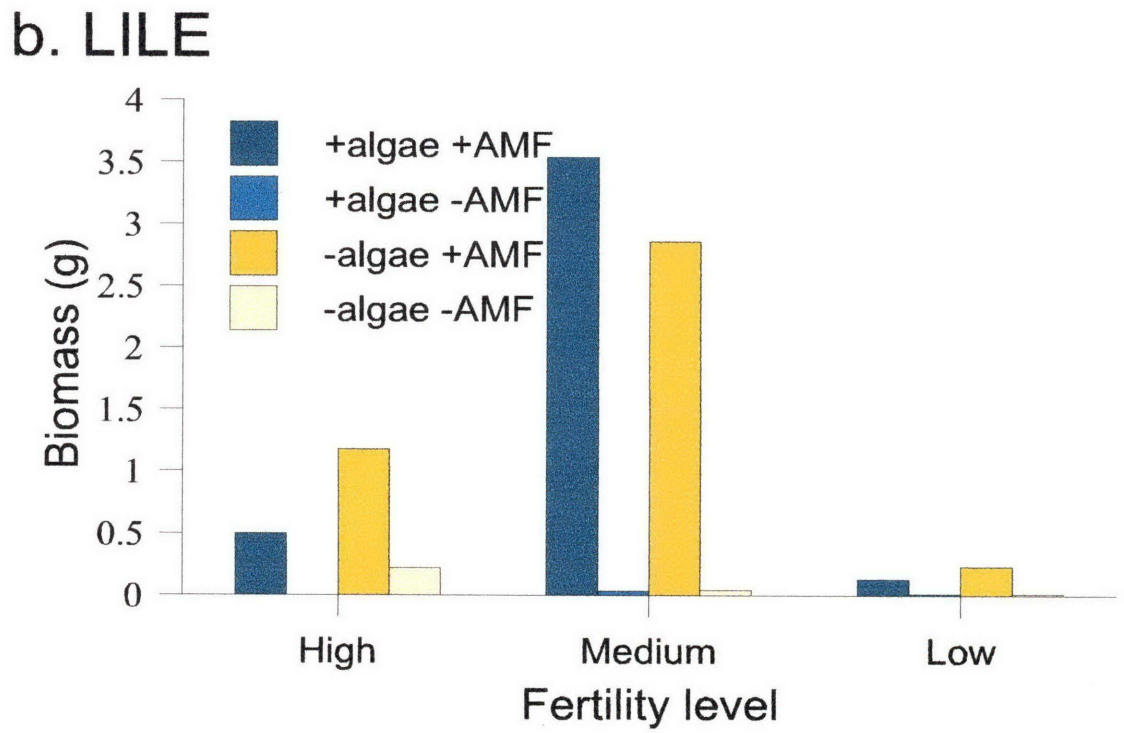
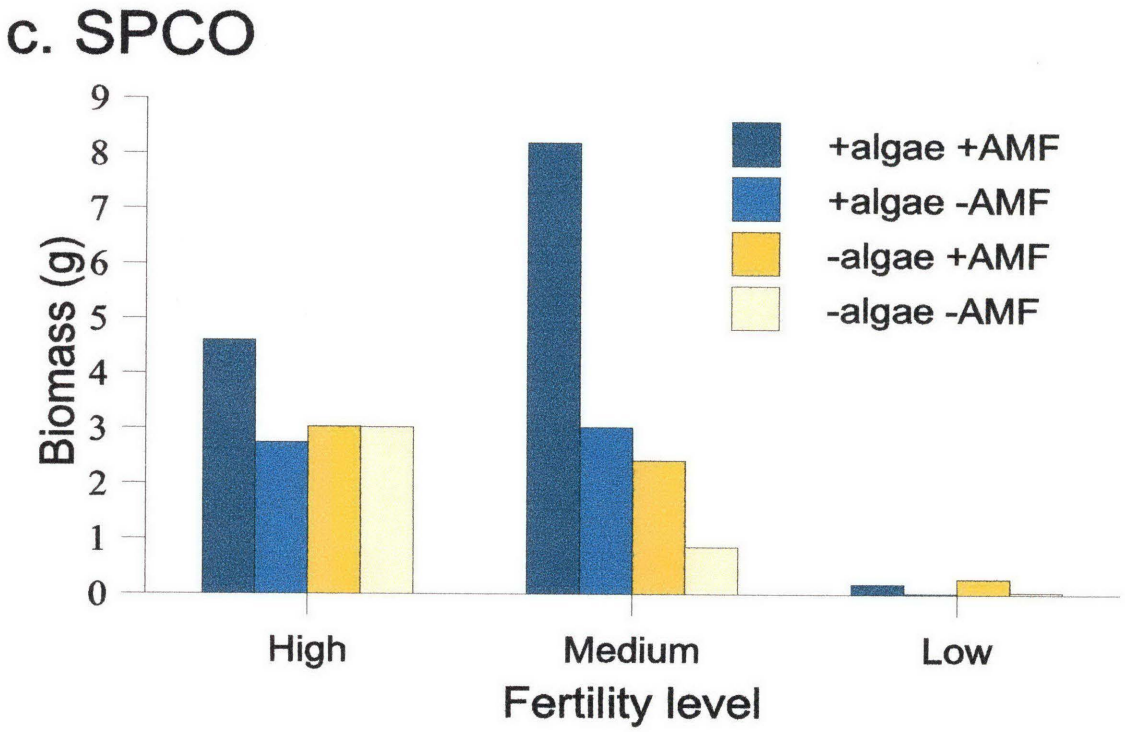


Figure 8 (continued).



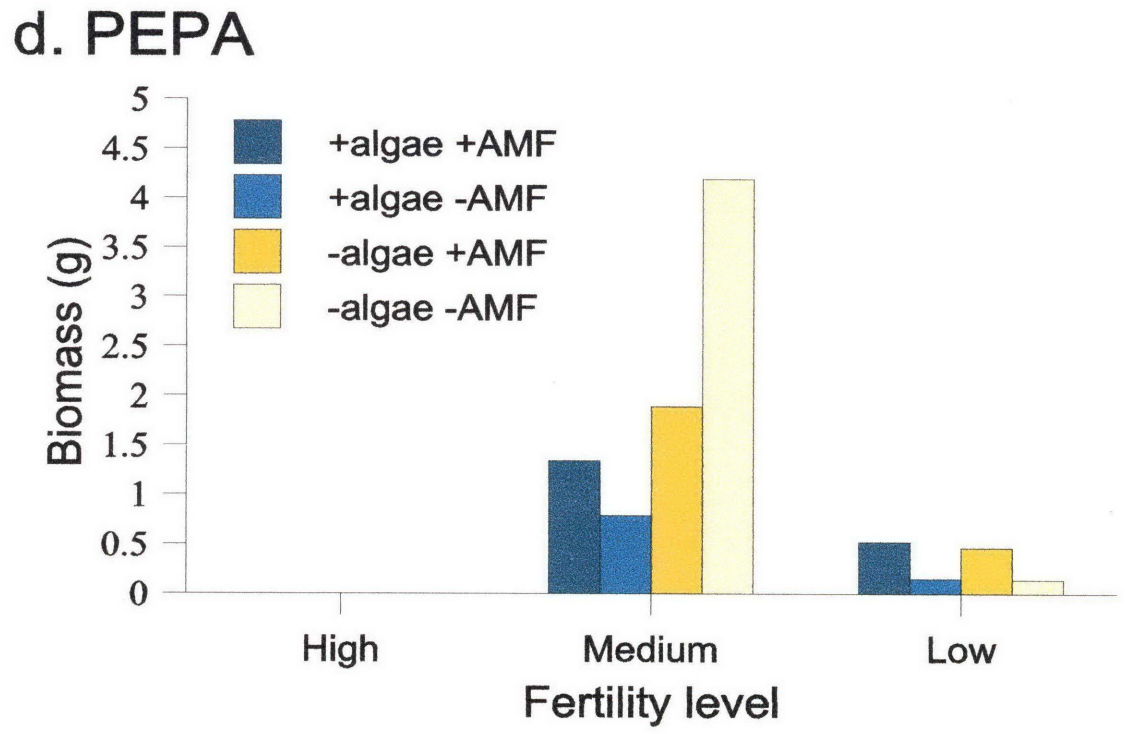
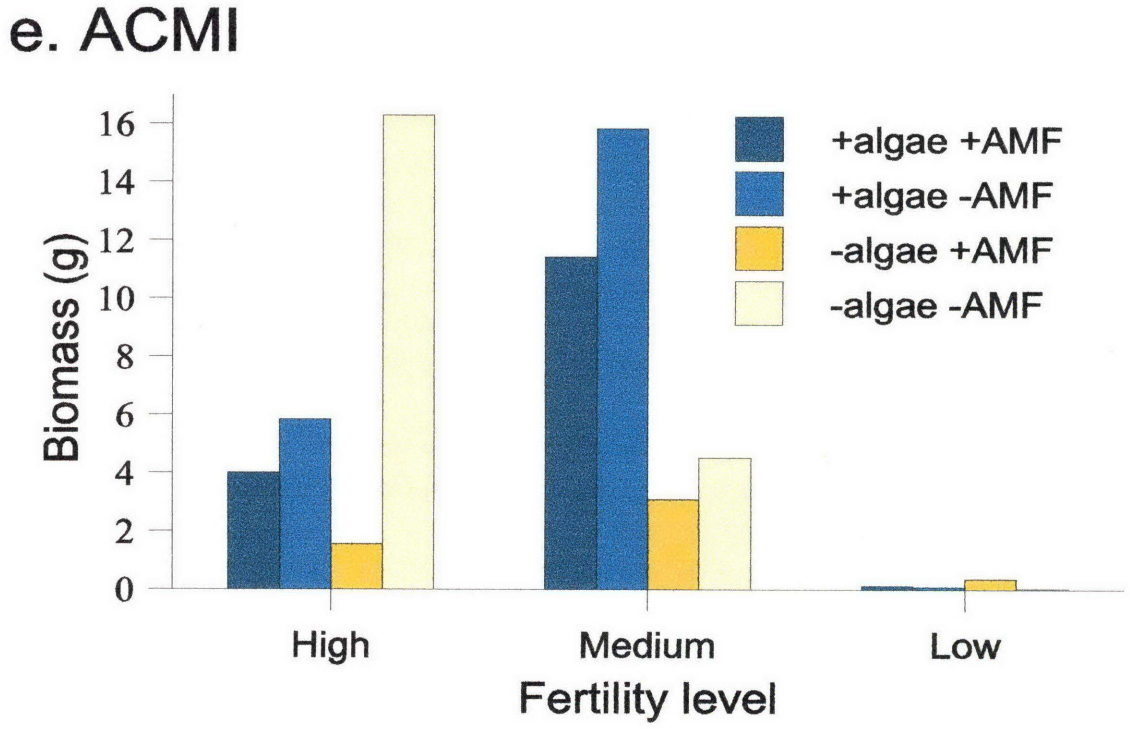


Figure 8 (continued).



In summary, growth of all plant species except PEPA was enhanced by algal inoculum at the medium fertility level, but tended to be decrease growth at low fertility. In PEPA, the reverse was true. Mycorrhizal inoculum enhanced growth of LILE and SPCO at all fertility levels, but negatively affected growth of HEBO plants. The result was that dual inoculation provided the greatest growth of SPCO and LILE plants at medium fertility, while mycorrhizae alone gave the greatest growth at low fertility. HEBO plants grew best without mycorrhizae, having benefited by algal inoculation at medium fertility, but not at low. In ACMI, nonmycorrhizal plants with algae grew best at medium fertility, with mycorrhizae alone providing the least growth. At low fertility, the reverse was true. Plants inoculated with mycorrhizae only grew best, followed by those inoculated with algae. Pepa plants did best without any inoculation treatments at medium fertility and best with dual inoculation at low fertility.

Plant reproduction was significantly affected by soil fertility, mycorrhizal inoculation, and their interaction in HEBO (Appendix III). Flower formation was greatest at the medium fertility level where vegetative growth was also greatest. Reproduction in HEBO occurred only in the absence of mycorrhizal inoculation except for a small amount at the lowest fertility level. Again, results may have been different with the inclusion of rhizobia. Algal inoculation appeared to enhance reproductive output (Figure 9a,b).

Reproduction in SPCO was also significantly affected by soil fertility, as well as by fertility interactions with AMF and algae (Appendix III). Flowering occurred only at the high and medium fertility levels. At high fertility, the greatest reproduction occurred in the absence of soil inoculation treatments, followed by those to which algae had been added (Figure 9c). At medium fertility, the greatest reproductive output occurred in dual-inoculated plants. Reproductive output in SPCO mirrors vegetative growth at medium fertility, though not at high.

Root/shoot ratio--The proportion of plant biomass invested in root tissue decreased substantially with increasing soil fertility. Fertility was highly significant ($p=0.0001$) in four of the five species (see Appendix III). *Sphaeralcea*, though nonsignificant, exhibited a similar trend. In all species, ratio values at low soil fertility were two to three times greater than those for medium and high levels (Figure 10). Similar findings have been detailed in previous experiment reports (McArthur, Pendleton, and Pendleton 1995; Pendleton and Pendleton 1995) and by other researchers (Chapin 1980; Redente, Friedlander, and McLendon 1992). This decrease in root/shoot ratio in interpreted to mean that, under conditions of increased nutrient availability, proportionately less of the root system is needed to meet the demand for plant growth (Kachi and Rorison 1989).

Figure 9. Reproductive output of *Sphaeralcea* and nonmycorrhizal *Hedysarum* plants.

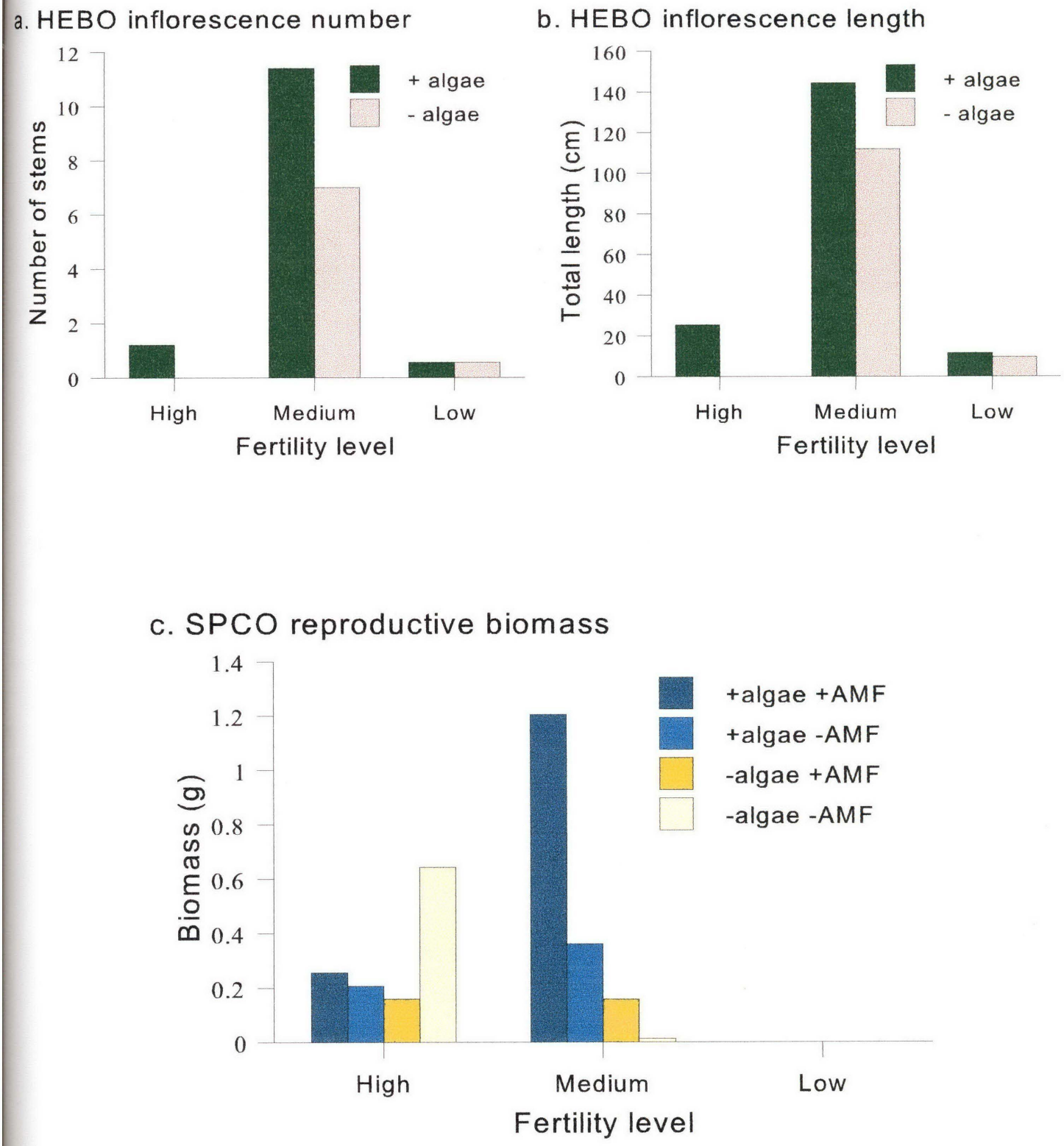


Figure 10. Root/shoot ratios as a function of soil fertility level.

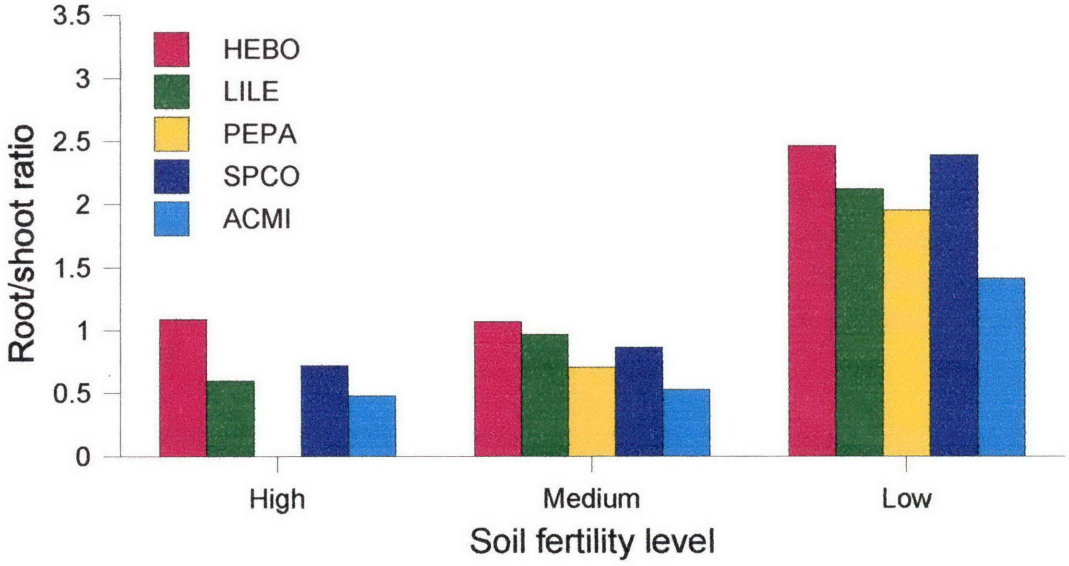
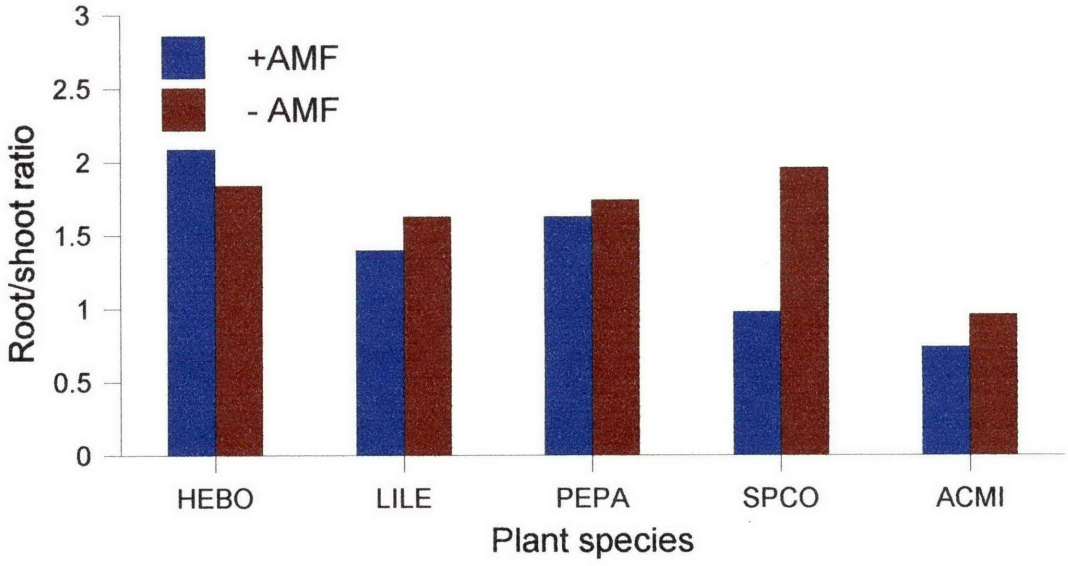


Figure 11. Root/shoot ratios of mycorrhizal and nonmycorrhizal plants.



The addition of mycorrhizal inoculum significantly reduced root/shoot ratios in some cases. Root/shoot ratios of *Linum, Sphaeralcea* and *Achillea* were consistently reduced in mycorrhizal plants at all soil fertility levels (Figure 11). These differences were significant overall in Lile ($p=0.0010$) and Acmi ($p=0.0005$), and significant at the medium fertility level in Spco ($p=0.0002$). In *Hedysarum* and *Penstemon*, mycorrhizal plants tended to have higher root/shoot ratios at high soil fertility and lower ratios at low soil fertility than their nonmycorrhizal counterparts. In previous studies, we have found lower r/s values, especially at low soil fertility, in other forbs (McArthur, Pendleton, and Pendleton 1995). Mycorrhizal fungi provide an extension of the plant root system and are presumed to be more efficient at extracting soil nutrients, particularly at low levels of phosphorus.

Algal inoculation had little effect on root/shoot ratio. Significant effects were observed in only three instances. Inoculated *Sphaeralcea* plants had consistently lower ratios than uninoculated plants, this difference being significant at the medium fertility level ($p=0.0002$). In *Penstemon*, algae and mycorrhizal inoculation interacted significantly at low fertility, with algae reducing the r/s ratio in nonmycorrhizal plants. In contrast, ratios in *Linum* were significantly increased by inoculation with blue-green algae ($p=0.0014$). At this point, there appears to be no consistent effect of algal inoculation on root/shoot biomass ratios.

Conclusions--A summary of research findings on the effect of microphytic crust inoculation and arbuscular mycorrhizal fungi on productivity of Intermountain forb species is given below.

- Survival, growth, and reproduction of Intermountain forbs were significantly affected by additions of mycorrhizal and algal inocula. Effects varied with soil fertility level.

- Growth of all plant species was enhanced by the addition of fertilizer. Greatest plant growth occurred at the medium fertility. Percentage survival, however, decreased significantly with fertilizer additions. Growth should not be the only factor used in evaluating revegetation efforts.

- The addition of algal inoculum significantly improved plant survival at medium and low soil fertility. Overall plant survival ranged from a high of 81.9% in ACMI plants to 35.4% in PEPA.

- Inoculation with blue-green algae also enhanced growth of ACMI, HEBO, LILE, and SPCO plants at medium fertility, and nonmycorrhizal ACMI plants at low fertility. Algal inoculation decreased growth of PEPA plants at medium fertility.

- Forb species differed in their response to mycorrhizal inoculum. LILE and SPCO plants appear to be highly dependent on mycorrhizal fungi, growing best in the presence of AMF inoculum, particularly at low soil fertility. ACMI and PEPA responded positively to mycorrhizal fungi at low soil fertility, but were negatively affected or unchanged at medium and high fertility. HEBO responded negatively to mycorrhizal inoculum, however rhizobial inoculum was not included in the experiment.

- Best growth at medium soil fertility was obtained under dual inoculation for SPCO and LILE plants. HEBO and ACMI plants grew best with algae alone. PEPA experienced greatest growth in the uninoculated control treatment. At low fertility, HEBO grew best in the uninoculated control treatment. All other species attained their greatest growth with mycorrhizal inoculum alone.

- The proportion of plant biomass invested in root tissue decreased with increasing soil fertility. Additions of mycorrhizal inoculum also reduced root/shoot ratios in ACMI. LILE, and SPCO. HEBO and PEPA ratios were reduced in mycorrhizal plants only at low soil fertility. Algal inoculation had no consistent effect of root/shoot ratios.

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Appendix IA. Attained significance values for treatment effects on ARFI growth measures using General Linear Models.

Source	shoot biomass	root biomass	r/s ratio
Fertilizer level	0.0001**	0.0001**	0.0004**
BRTE competition	0.0001**	0.0002**	0.0783
Algal inoculation	0.7945	0.4157	0.7068
AMF inoculation	0.0639	0.0271*	0.3236
Fert x comp	0.0001**	0.0007**	0.7377
Fert x algae	0.6678	0.9684	0.9933
Fert x AMF	0.0346*	0.0257*	0.9903
Algae x comp	0.4646	0.2472	0.4937
AMF x comp	0.6005	0.4443	0.0352*
Algae x AMF	0.5995	0.4221	0.0304*

Appendix IB. Attained significance values for treatment effects on ARTR growth measures using General Linear Models.

Source	shoot biomass	root biomass	r/s ratio
Fertilizer level	0.0004**	0.0003**	0.0002**
BRTE competition	0.1353	0.0737	0.2711
Algal inoculation	0.0617	0.1679	0.9236
AMF inoculation	0.7616	0.5056	0.1783
Fert x comp	0.0647	0.0503	0.6343
Fert x algae	0.4675	0.7031	0.9561
Fert x AMF	0.4813	0.5394	0.1610
Algae x comp	0.6095	0.7428	0.6565
AMF x comp	0.8851	0.8391	0.2406
Algae x AMF	0.8740	0.9859	0.9573

Appendix IC. Attained significance values for treatment effects on CHNA growth measures using General Linear Models.

Source	shoot biomass	root biomass	r/s ratio
Fertilizer level	0.0030**	0.0233*	0.0083**
BRTE competition	0.1390	0.1994	0.2091
Algal inoculation	0.1575	0.2781	0.1848
AMF inoculation	0.8799	0.9333	0.1567
Fert x comp	0.0681	0.2946	0.0547
Fert x algae	0.0178*	0.1226	0.0903
Fert x AMF	0.9870	0.5355	0.1379
Algae x comp	0.3157	0.3582	0.1755
AMF x comp	0.8385	0.9851	0.5434
Algae x AMF	0.1284	0.0182*	0.0193*

Appendix ID. Attained significance values for treatment effects on CORA growth measures using General Linear Models.

Source	shoot biomass	root biomass	r/s ratio
Fertilizer level	0.4601	0.0071**	0.5787
BRTE competition	0.4985	0.0013**	0.1668
Algal inoculation	0.7432	0.4879	0.6714
AMF inoculation	0.5127	0.4831	0.3303
Fert x comp	-	-	-
Fert x algae	0.8256	0.1052	0.9885
Fert x AMF	0.0931	0.0229*	0.6837
Algae x comp	0.5277	0.0694	0.7886
AMF x comp	0.6160	0.7816	0.1620
Algae x AMF	0.7000	0.7022	0.8291

Appendix IE. Attained significance values for treatment effects on EPVI growth measures using General Linear Models.

Source	shoot biomass	root biomass	r/s ratio
Fertilizer level	0.2711	0.1433	0.0390*
BRTE competition	0.0003**	0.0033**	0.2852
Algal inoculation	0.3493	0.3634	0.9221
AMF inoculation	0.1567	0.4480	0.4280
Fert x comp	-	-	-
Fert x algae	0.7181	0.5006	0.1113
Fert x AMF	0.2818	0.8721	0.5038
Algae x comp	0.5732	0.4993	0.2241
AMF x comp	0.3789	0.8622	0.2787
Algae x AMF	0.3905	0.8138	0.5177

Appendix IF. Attained significance values for treatment effects on BRTE growth measures using General Linear Models.

Source	shoot biomass	root biomass	r/s ratio
Fertilizer level	0.0001**	0.0001**	0.0014**
Algal inoculation	0.1422	0.2022	0.2822
AMF inoculation	0.4144	0.5654	0.1578
Shrub species	0.1294	0.0397*	0.3409
Fert x algae	0.5279	0.5885	0.7863
Fert x AMF	0.2457	0.7910	0.0234*
Algae x AMF	0.9912	0.5792	0.9225
Fert x shrub	0.6055	0.5508	0.2122
AMF x shrub	0.9667	0.2202	0.2542
Algae x shrub	0.5170	0.3102	0.0857

Appendix IIA. Summary of ARFI growth measures.

	+ Brte				- Brte			
	n	shoot wt.	root wt.	r/s ratio	n	shoot wt.	root wt.	r/s ratio
High								
+ algae								
+ AMF	-	-	-	-	3	2.838	0.396	0.14
- AMF	3	0.606	0.080	0.13	2	6.237	1.106	0.18
- algae								
+ AMF	-	-	-	-	3	4.299	0.880	0.20
- AMF	2	0.129	0.009	0.07	3	4.600	1.005	0.22
Medium								
+ algae								
+ AMF	1	0.270	0.025	0.09	3	6.592	0.830	0.13
- AMF	-	-	-	-	3	10.216	1.940	0.19
- algae								
+ AMF	-	-	-	-	3	5.346	1.002	0.19
- AMF	1	0.182	0.036	0.20	3	10.133	2.033	0.20
Low								
+ algae								
+ AMF	2	0.026	0.007	1.28	1	0.024	0.028	1.16
- AMF	1	0.256	0.014	0.06	3	0.170	0.056	0.33
- algae								
+ AMF	3	0.061	0.009	0.14	3	0.263	0.097	0.37
- AMF	1	0.015	0.016	1.10	3	0.210	0.103	0.49

Appendix IIB. Summary of ARTR growth measures.

	+ Brte				- Brte			
	n	shoot wt.	root wt.	r/s ratio	n	shoot wt.	root wt.	r/s ratio
High								
+ algae								
+ AMF	-	-	-	-	3	3.503	0.605	0.17
- AMF	-	-	-	-	3	5.943	0.997	0.17
- algae								
+ AMF	-	-	-	-	1	3.819	0.608	0.16
- AMF	-	-	-	-	3	1.589	0.422	0.27
Medium								
+ algae								
+ AMF	1	0.278	0.059	0.21	2	7.017	1.180	0.17
- AMF	-	-	-	-	3	3.840	0.760	0.20
- algae								
+ AMF	1	0.463	0.050	0.11	3	3.183	0.683	0.21
- AMF	-	-	-	-	3	3.311	0.736	0.22
Low								
+ algae								
+ AMF	1	0.033	0.039	1.19	3	0.037	0.028	0.75
- AMF	2	0.017	0.018	1.03	3	0.102	0.081	0.79
- algae								
+ AMF	-	-	-	-	-	-	-	-
- AMF	1	0.002	0.002	0.94	1	0.007	0.012	1.75

Appendix IIC. Summary of CHNA growth measures.

	+ Brte				- Brte			
	n	shoot wt.	root wt.	r/s ratio	n	shoot wt.	root wt.	r/s ratio
High								
+ algae								
+ AMF	1	0.179	0.073	0.41	3	2.150	0.307	0.14
- AMF	-	-	-	-	2	2.788	0.681	0.24
- algae								
+ AMF	1	0.112	0.077	0.69	1	0.936	0.298	0.32
- AMF	-	-	-	-	3	0.378	0.089	0.24
Medium								
+ algae								
+ AMF	-	-	-	-	2	0.285	0.041	0.14
- AMF	-	-	-	-	1	1.428	0.453	0.32
- algae								
+ AMF	-	-	-	-	2	1.807	0.544	0.30
- AMF	-	-	-	-	2	0.950	0.118	0.12
Low								
+ algae								
+ AMF	1	0.104	0.049	0.48	2	0.205	0.160	0.78
- AMF	-	-	-	-	1	0.006	0.026	4.45
- algae								
+ AMF	2	0.032	0.015	0.46	2	0.068	0.042	0.62
- AMF	2	0.003	0.003	0.86	2	0.063	0.030	0.49

Appendix IID. Summary of CORA growth measures.

	+ Brte				- Brte			
	n	shoot wt.	root wt.	r/s ratio	n	shoot wt.	root wt.	r/s ratio
High								
+ algae								
+ AMF	-	-	-	-	-	-	-	-
- AMF	-	-	-	-	1	0.215	0.065	0.30
- algae								
+ AMF	-	-	-	-	3	0.100	0.017	0.17
- AMF	-	-	-	-	-	-	-	-
Medium								
+ algae								
+ AMF	-	-	-	-	2	0.085	0.016	0.19
- AMF	-	-	-	-	2	0.272	0.040	0.15
- algae								
+ AMF	-	-	-	-	1	0.111	0.015	0.13
- AMF	-	-	-	-	3	0.201	0.030	0.15
Low								
+ algae								
+ AMF	1	0.128	0.075	0.59	1	0.100	0.059	0.59
- AMF	2	0.106	0.029	0.27	-	-	-	-
- algae								
+ AMF	3	0.103	0.048	0.46	3	0.187	0.100	0.56
- AMF	3	0.081	0.025	0.31	3	0.104	0.064	0.62

Appendix IIE. Summary of EPVI growth measures.

	+ Brte				- Brte			
	n	shoot wt.	root wt.	r/s ratio	n	shoot wt.	root wt.	r/s ratio
High								
+ algae								
+ AMF	-	-	-	-	-	-	-	-
- AMF	-	-	-	-	-	-	-	-
- algae								
+ AMF	-	-	-	-	2	0.084	0.024	0.28
- AMF	-	-	-	-	2	0.034	0.018	0.51
Medium								
+ algae								
+ AMF	-	-	-	-	2	0.044	0.018	0.42
- AMF	-	-	-	-	2	0.022	0.016	0.76
- algae								
+ AMF	-	-	-	-	2	0.040	0.016	0.39
- AMF	-	-	-	-	3	0.049	0.017	0.35
Low								
+ algae								
+ AMF	2	0.032	0.020	0.65	2	0.091	0.062	0.68
- AMF	2	0.018	0.010	0.57	1	0.076	0.035	0.45
- algae								
+ AMF	3	0.047	0.029	0.62	3	0.081	0.085	1.05
- AMF	3	0.028	0.018	0.66	1	0.104	0.078	0.76

Appendix IIF. Summary of BRTE growth measures.

	ARFI				ARTR			
	n	shoot wt.	root wt.	r/s ratio	n	shoot wt.	root wt.	r/s ratio
High								
+ algae								
+ AMF	3	22.600	14.451	0.64	3	26.567	16.865	0.63
- AMF	3	22.433	7.061	0.31	3	24.967	7.510	0.30
- algae								
+ AMF	3	15.100	3.082	0.20	3	17.630	5.490	0.31
- AMF	3	24.833	8.486	0.34	3	20.433	22.404	1.10
Medium								
+ algae								
+ AMF	3	25.100	13.782	0.55	3	21.933	21.926	1.00
- AMF	3	14.867	4.980	0.34	3	21.700	16.220	0.75
- algae								
+ AMF	3	20.167	9.744	0.48	3	15.461	5.300	0.34
- AMF	3	19.800	10.004	0.51	3	21.333	25.276	1.18
Low								
+ algae								
+ AMF	3	0.766	0.626	0.82	3	1.200	0.863	0.72
- AMF	3	0.983	0.494	0.50	3	1.341	0.637	0.47
- algae								
+ AMF	3	0.896	0.848	0.95	3	0.597	0.336	0.56
- AMF	3	0.920	0.395	0.43	3	1.623	0.755	0.47

Appendix IIF cont. Summary of BRTE growth measures.

	CHNA				CORA			
	n	shoot wt.	root wt.	r/s ratio	n	shoot wt.	root wt.	r/s ratio
High								
+ algae								
+ AMF	3	20.233	6.938	0.34	3	33.500	14.292	0.43
- AMF	3	18.767	10.408	0.55	3	22.300	19.236	0.86
- algae								
+ AMF	3	19.233	14.777	0.77	3	17.867	5.584	0.31
- AMF	3	18.133	3.746	0.21	3	22.367	13.136	0.59
Medium								
+ algae								
+ AMF	3	14.200	5.786	0.41	3	15.033	16.839	1.12
- AMF	3	20.800	8.480	0.41	3	28.667	22.733	0.79
- algae								
+ AMF	3	21.000	17.152	0.82	3	25.067	12.779	0.51
- AMF	3	18.000	5.550	0.31	2	23.650	5.732	0.24
Low								
+ algae								
+ AMF	3	1.610	1.981	1.23	2	0.991	0.748	0.75
- AMF	3	1.079	1.398	1.30	3	1.544	1.456	0.94
- algae								
+ AMF	3	1.513	0.656	0.43	3	0.817	0.733	0.90
- AMF	3	1.822	0.594	0.33	3	1.511	0.908	0.60

Appendix IIF cont. Summary of BRTE growth measures.

	EPVI			
	n	shoot wt.	root wt.	r/s ratio
High				
+ algae				
+ AMF	3	16.167	4.847	0.30
- AMF	3	14.200	7.159	0.50
- algae				
+ AMF	3	25.533	9.176	0.36
- AMF	3	18.833	12.566	0.67
Medium				
+ algae				
+ AMF	3	16.167	9.205	0.57
- AMF	3	32.533	22.585	0.69
- algae				
+ AMF	2	18.585	15.679	0.84
- AMF	3	15.821	5.710	0.36
Low				
+ algae				
+ AMF	3	0.867	0.649	0.75
- AMF	3	1.372	0.696	0.51
- algae				
+ AMF	3	0.910	1.318	0.45
- AMF	3	1.509	1.230	0.82

Appendix IIIA. Attained significance values for treatment effects on ACMI growth measures using General Linear Models.

Source	shoot biomass	root biomass	r/s ratio
Fertilizer level	0.0001**	0.0001**	0.0001**
AMF inoculation	0.0009**	0.0015**	0.0001**
Algal inoculation	0.0290*	0.0342*	0.0691
Fert x AMF	0.0001**	0.0010**	0.0005**
Fert x algae	0.0001**	0.0001**	0.5737
AMF x algae	0.1769	0.7378	0.3332

Appendix IIIB. Attained significance values for treatment effects on HEBO growth measures using General Linear Models.

Source	shoot biomass	root biomass	r/s ratio	$\bar{x}$ no. inflorescence	total inflorescence length
Fertilizer level	0.0001**	0.0005**	0.0001**	0.0001**	0.0003**
AMF inoculation	0.0056**	0.0133*	0.5676	0.0110*	0.0173*
Algal inoculation	0.7639	0.8460	0.2637	0.3863	0.6089
Fert x AMF	0.0021**	0.0972	0.4962	0.0013**	0.0047**
Fert x algae	0.2175	0.2190	0.2097	0.2804	0.6030
AMF x algae	0.9656	0.9844	0.7003	0.6040	0.7634

Appendix IIIC. Attained significance values for treatment effects on LILE growth measures using General Linear Models.

Source	shoot biomass	root biomass	r/s ratio
Fertilizer level	0.0041**	0.0362*	0.0001**
AMF inoculation	0.0001**	0.0001**	0.0010**
Algal inoculation	0.9153	0.8429	0.0014**
Fert x AMF	0.0001**	0.0002**	0.3439
Fert x algae	0.7455	0.8414	0.7413
AMF x algae	0.7642	0.9941	0.7155

Appendix IIID. Attained significance values for treatment effects on PEPA growth measures using General Linear Models.

Source	shoot biomass	root biomass	r/s ratio
Fertilizer level	0.0001**	0.0006**	0.0001**
AMF inoculation	0.8496	0.0133*	0.1461
Algal inoculation	0.0501*	0.4852	0.6643
Fert x AMF	0.0175*	0.3553	0.0795
Fert x algae	0.0002**	0.0037**	0.5690
AMF x algae	0.2051	0.2045	0.0438*

Appendix IIIE. Attained significance values for treatment effects on SPCO growth measures using General Linear Models.

Source	shoot biomass	root biomass	r/s ratio	repro. wt.
Fertilizer level	0.0001**	0.0001**	0.1523	0.0004**
AMF inoculation	0.0285*	0.1662	0.2515	0.5680
Algal inoculation	0.0140*	0.1194	0.1060	0.1384
Fert x AMF	0.0654	0.1954	0.5374	0.0319*
Fert x algae	0.0034**	0.0301*	0.2781	0.0025**
AMF x algae	0.1972	0.7465	0.1439	0.1318

Appendix IVA. Attained significance values for treatment effects on ACMI growth measures by fertilizer level.

Fertility/Source	shoot biomass	root biomass	r/s ratio
High fertility			
AMF inoculation	0.0001**	0.0002**	0.0072**
Algal inoculation	0.0097**	0.0133*	0.8980
AMF x algae	0.0023**	0.0052**	0.0689
Medium fertility			
AMF inoculation	0.4895	0.1841	0.0725
Algal inoculation	0.0001**	0.0001**	0.0019**
AMF x algae	0.4216	0.1155	0.0902
Low fertility			
AMF inoculation	0.0001**	0.0020**	0.0001**
Algal inoculation	0.0023**	0.1011	0.5849
AMF x algae	0.0001**	0.0282*	0.2926

Appendix IVB. Attained significance values for treatment effects on HEBO growth measures by fertilizer level.

Fertility/Source	shoot biomass	root biomass	r/s ratio	$\bar{x}$ no. inflorescence	total inflorescence length
High fertility					
AMF inoculation	--	--	--	--	--
Algal inoculation	--	--	--	--	--
AMF x algae	--	--	--	--	--
Medium fertility					
AMF inoculation	0.0231*	0.0900	0.7301	0.0320*	0.0511
Algal inoculation	0.5268	0.5820	0.5049	0.4933	0.7321
AMF x algae	0.9719	0.9708	0.0681	0.6221	0.8060
Low fertility					
AMF inoculation	0.0289*	0.0527	0.4863	0.0652	0.0723
Algal inoculation	0.0463*	0.1378	0.1607	0.8618	0.9782
AMF x algae	0.7529	0.9825	0.8142	0.8647	0.7694

Appendix IVC. Attained significance values for treatment effects on LILE growth measures by fertilizer level.

Fertility/Source	shoot biomass	root biomass	r/s ratio
High fertility			
AMF inoculation	0.0202*	0.1188	0.0022**
Algal inoculation	0.2529	0.4340	0.6049
AMF x algae	--	--	--
Medium fertility			
AMF inoculation	0.0028**	0.0043**	0.0003**
Algal inoculation	0.7954	0.8350	0.1068*
AMF x algae	0.7169	0.8195	0.3659
Low fertility			
AMF inoculation	0.0001**	0.0001**	0.1395
Algal inoculation	0.0588	0.1693	0.0226*
AMF x algae	0.1386	0.2598	0.9970

Appendix IVD. Attained significance values for treatment effects on PEPA growth measures by fertilizer level.

Fertility/Source	shoot biomass	root biomass	r/s ratio
High fertility			
AMF inoculation	--	--	--
Algal inoculation	--	--	--
AMF x algae	--	--	--
Medium fertility			
AMF inoculation	0.3757	0.8610	0.0111*
Algal inoculation	0.0798	0.1515	0.2973
AMF x algae	0.2684	0.6290	0.5153
Low fertility			
AMF inoculation	0.0001**	0.0005**	0.0561
Algal inoculation	0.6309	0.2600	0.5504
AMF x algae	0.7860	0.1869	0.0312*

Appendix IVE. Attained significance values for treatment effects on SPCO growth measures by fertilizer level.

Fertility/Source	shoot biomass	root biomass	r/s ratio	repro. biomass
High fertility				
AMF inoculation	0.6275	0.8762	0.0806	0.2393
Algal inoculation	0.6736	0.8440	0.1876	0.5072
AMF x algae	0.5787	0.7995	0.7230	0.2604
Medium fertility				
AMF inoculation	0.0125*	0.1541	0.0108*	0.1423
Algal inoculation	0.0005**	0.0310*	0.0002**	0.0107*
AMF x algae	0.1543	0.8611	0.3053	0.2796
Low fertility				
AMF inoculation	0.0001**	0.0001**	0.3119	--
Algal inoculation	0.1340	0.0751	0.1545	--
AMF x algae	0.3513	0.6644	0.1444	--

Appendix VA. Summary of ACMI growth measures.

	n	shoot wt.	root wt.	r/s ratio
High				
+ algae				
+ AMF	6	4.005	1.899	0.45
- AMF	7	5.828	2.712	0.48
- algae				
+ AMF	6	1.555	0.554	0.34
- AMF	12	16.275	9.360	0.57
Medium				
+ algae				
+ AMF	12	11.413	6.006	0.49
- AMF	12	15.817	11.188	0.68
- algae				
+ AMF	5	3.089	1.733	0.44
- AMF	12	4.523	2.118	0.45
Low				
+ algae				
+ AMF	12	0.128	0.174	1.22
- AMF	12	0.082	0.121	1.72
- algae				
+ AMF	12	0.368	0.369	0.99
- AMF	10	0.044	0.085	1.80

Appendix VB. Summary of HEBO growth measures.

	n	shoot wt.	root wt.	r/s ratio	$\bar{x}$ no. inflorescence	total inflorescence length
High						
+ algae						
+ AMF	--	--	--	--	--	--
- AMF	5	6.873	7.649	1.09	1.200	25.40
- algae						
+ AMF	--	--	--	--	--	--
- AMF	--	--	--	--	--	--
Medium						
+ algae						
+ AMF	4	4.297	5.878	0.86	0.000	0.00
- AMF	10	11.321	12.250	1.10	11.400	144.65
- algae						
+ AMF	3	2.638	4.096	1.47	0.000	0.00
- AMF	5	9.452	10.194	0.97	7.000	111.90
Low						
+ algae						
+ AMF	12	1.047	2.622	2.58	0.000	0.00
- AMF	11	1.637	4.412	2.69	0.546	11.50
- algae						
+ AMF	11	1.587	3.999	2.18	0.091	1.40
- AMF	11	2.373	5.829	2.41	0.546	9.72

Appendix VC. Summary of LILE growth measures.

	n	shoot wt.	root wt.	r/s ratio
High				
+ algae				
+ AMF	1	0.498	0.222	0.45
- AMF	--	--	--	--
- algae				
+ AMF	4	1.184	0.381	0.35
- AMF	7	0.219	0.174	0.76
Medium				
+ algae				
+ AMF	4	3.545	1.779	0.53
- AMF	9	0.035	0.051	1.45
- algae				
+ AMF	3	2.856	1.525	0.29
- AMF	5	0.040	0.030	0.87
Low				
+ algae				
+ AMF	12	0.129	0.237	2.22
- AMF	12	0.009	0.023	2.50
- algae				
+ AMF	9	0.226	0.366	1.64
- AMF	5	0.013	0.024	1.91

Appendix VD. Summary of PEPA growth measures.

	n	shoot wt.	root wt.	r/s ratio
High				
+ algae				
+ AMF	--	--	--	--
- AMF	--	--	--	--
- algae				
+ AMF	--	--	--	--
- AMF	--	--	--	--
Medium				
+ algae				
+ AMF	2	1.344	1.172	0.93
- AMF	3	0.793	0.527	0.68
- algae				
+ AMF	2	1.887	1.888	0.91
- AMF	4	4.189	2.034	0.53
Low				
+ algae				
+ AMF	11	0.520	1.056	1.92
- AMF	9	0.152	0.297	1.86
- algae				
+ AMF	9	0.464	0.685	1.60
- AMF	10	0.137	0.332	2.43

Appendix VE. Summary of SPCO growth measures.

	n	shoot wt.	root wt.	r/s ratio	repro. wt.
High					
+ algae					
+ AMF	6	4.595	2.045	0.55	0.256
- AMF	5	2.742	1.946	0.75	0.206
- algae					
+ AMF	8	3.028	1.739	0.71	0.159
- AMF	8	3.016	1.996	0.84	0.643
Medium					
+ algae					
+ AMF	10	8.213	4.397	0.59	1.204
- AMF	11	3.016	2.690	0.95	0.360
- algae					
+ AMF	9	2.415	2.428	1.00	0.157
- AMF	3	0.845	1.030	1.17	0.012
Low					
+ algae					
+ AMF	11	0.183	0.268	1.37	0.000
- AMF	12	0.017	0.021	1.18	0.000
- algae					
+ AMF	9	0.276	0.347	1.46	0.000
- AMF	7	0.038	0.149	7.35	0.000

Appendix VI. Percent survival of five herbaceous Intermountain plant species by treatment.

	+ algae		- algae	
	+ AMF	- AMF	+ AMF	- AMF
Achillea millefolium				
High	50.0	58.3	50.0	100.0
Medium	100.0	100.0	41.7	100.0
Low	100.0	100.0	100.0	83.3
Hedysarum boreale				
High	0.0	50.0	0.0	0.0
Medium	25.0	83.3	25.0	41.7
Low	100.0	91.7	91.7	91.7
Linium lewisii				
High	8.3	0.0	33.3	58.3
Medium	33.3	75.0	25.0	41.7
Low	100.0	100.0	75.0	41.7
Penstemon palmeri				
High	0.0	0.0	0.0	0.0
Medium	16.7	25.0	16.7	33.3
Low	91.7	83.3	75.0	83.3
Sphaeralcea coccinea				
High	50.0	50.0	66.7	66.7
Medium	83.3	91.7	75.0	25.0
Low	91.7	100.0	75.0	58.3

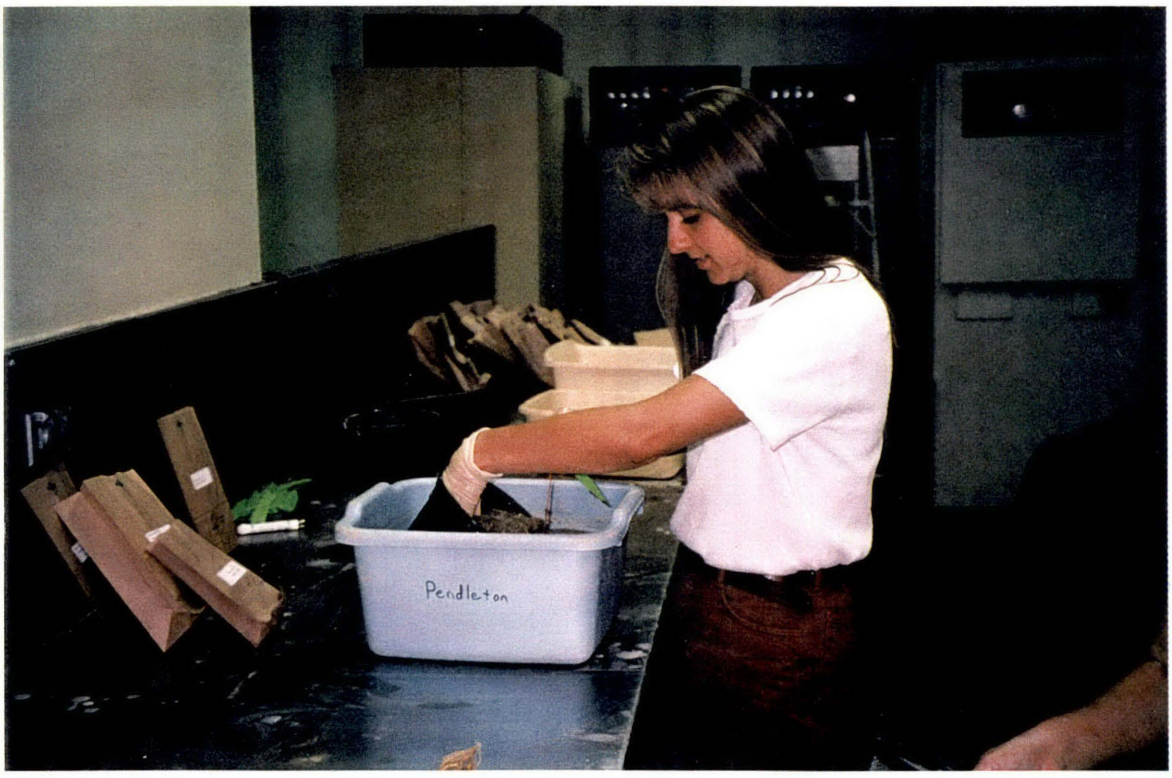
Greenhouse cleanup

Preparation of mycorrhizal inoculum

Transplanting *Sphaeralcea*

Overview of 1996 experiment

Algal-inoculated pot



Harvesting

Achillea

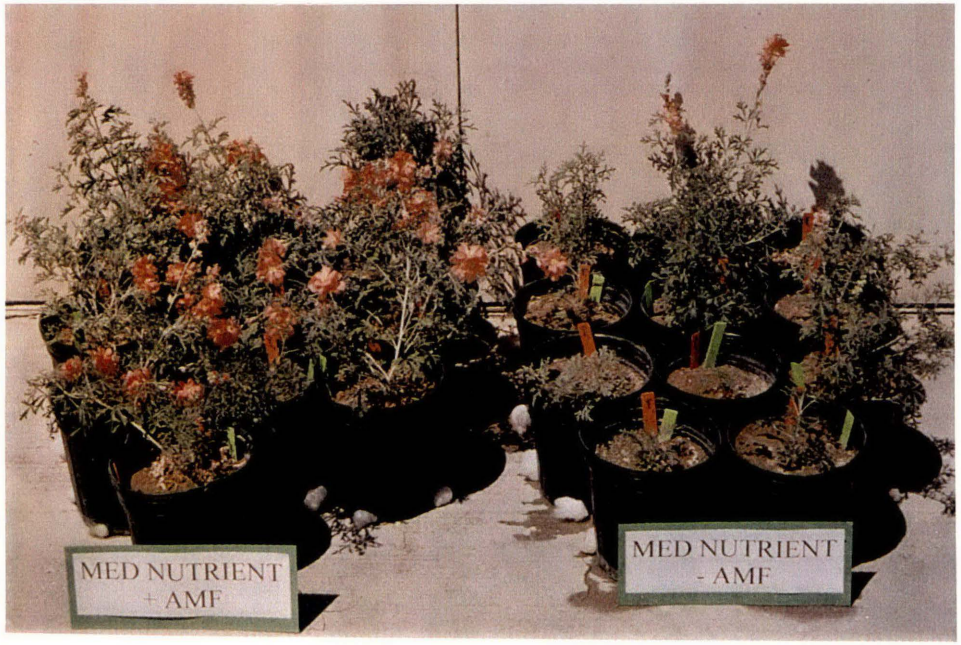
Hedysarum

Linum

Sphaeralcea

Negative response of *Hedysarum* to AMF
most pronounced at higher soil fertility

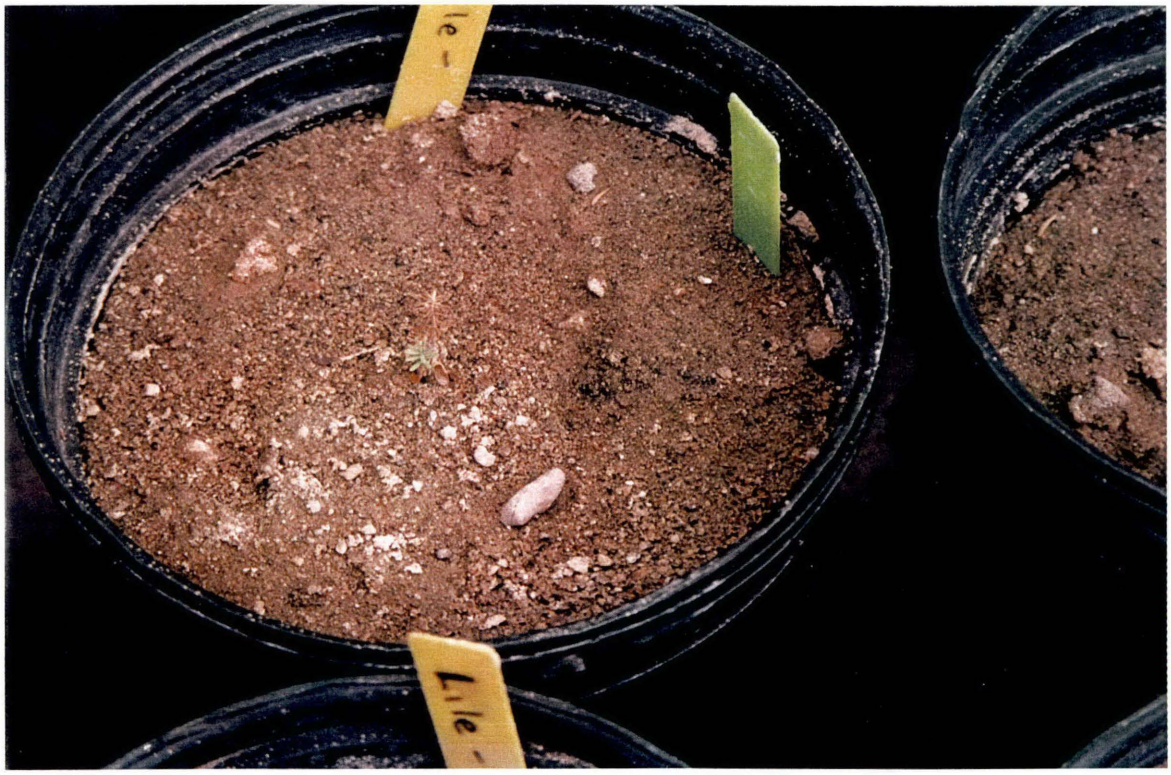
At low fertility, *Penstemon* grew best with both algae (green tags) and AMF (+)



Response of *Sphaeralcea* to mycorrhizal fungi

Response of *Linum* to mycorrhizal fungi
at high and low soil fertility

Mycorrhizal *Linum* at low soil fertility with algae



Nonmycorrhizal *Linum* at low soil fertility with algae